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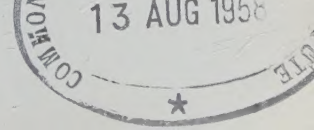

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DOPPLER MEASUREMENTS ON SOVIET SATELLITES

By A. H. ALLAN, Dominion Physical Laboratory, and
J. E. DRUMMOND, Applied Mathematics Laboratory,
Department of Scientific and Industrial Research, Wellington

(Received for publication, 1 April 1958)

Summary

Measurements of the Doppler change in frequency during the passage of the transmitters on the first two Soviet satellites have been successfully used to predict the times and elevations at which the satellites could be seen and photographed.

INTRODUCTION

Persistent cloudy weather over New Zealand during much of the lifetimes of the Soviet satellites, Sputnik I and Sputnik II, prevented any continuous series of visual sightings or photographs. Observations of the radio signal received from the satellites were used to determine the character of the orbits and the rate of decrease of orbital time as the orbit shrank in diameter as a result of friction between the atmosphere and the satellites. A visual sighting of Sputnik I, fourteen days after the radio signals had ceased, showed that the calculations from the radio measurements had predicted the time of transit to within a minute.

THE RADIO MEASUREMENTS

The satellites carried 40 Mc/s continuous-wave transmitters whose drift in frequency appeared to be less than five parts in 10^6 per day.

This good regulation allowed significant measurements to be made of the Doppler change in frequency during each transit. The apparatus and method that were used are as follows:

A 40 Mc/s radio receiver was arranged with its input coupled both to the 10th harmonic of a 4 Mc/s crystal oscillator and to a dipole aerial which received the signal from the satellite.. The input to the receiver was therefore the sum of these two signals. Because they differed slightly in frequency, the sums of the two signals showed an amplitude modulation at the difference frequency. This modulation appeared as an audible tone in the output of the receiver. The arrangement gave a good ratio of signal to noise when the amplitude of the local 40 Mc/s signal was suitably adjusted.

When the approaching satellite was first detected, the crystal was tuned to give a frequency a little higher than that which was being received from the satellite, so that the output tone of the receiver was about 200 c/s. Thereafter, the frequency of the crystal was left unaltered, and as the satellite passed and moved away the Doppler shift caused the frequency of the output tone to rise to about 1500 c/s. This arrangement was easier to operate than if the tuning had allowed the output tone to pass through zero frequency.

The frequency of the output tone of the receiver was measured by listening at the same time to the output tone of an audio signal generator. This generator was adjusted till the two tones produced no audible beat. An observer could make these adjustments and record the frequency every 15 seconds during the transit of a satellite.

This measured frequency differed from the true Doppler shift by an additive constant, because the frequency of the crystal harmonic was not identical with that of the transmitter. It is possible to estimate this difference, and so derive a curve of actual Doppler shift. Figures 1 and 2 give such estimated curves for two successive transits of both Sputnik I and Sputnik II. From these measurements, curves of the rate of change of frequency were also derived as shown in Figs 1 and 2.

Random errors arising in the measurements are best judged by the scatter of the points on the curves. This scatter is small. A systematic error would arise from a steady drift in the frequency of the crystal oscillator or of the satellite's transmitter. The likely drift of the crystal does not exceed 0·03 cycles/sec^2. The drift of the transmitter, judged by its change from day to day, is still smaller. These errors are negligible, being less than 1% of the measured maximum rates of change. The curves of Figs 1 and 2 suggest that the instant of maximum rate of change can be estimated to an accuracy of ± 10 sec.

It is generally recognized that Doppler shift measurements are useful in tracking satellites; they were recommended in "Radio Moscow" (Vakhnin, 1957), and they are an important part of the technique used by the staff of the Mullard Observatory, Cambridge (Staff of the Mullard Observatory, 1957). The technique described here is of interest in that the satellite was tracked by Doppler measurements alone and

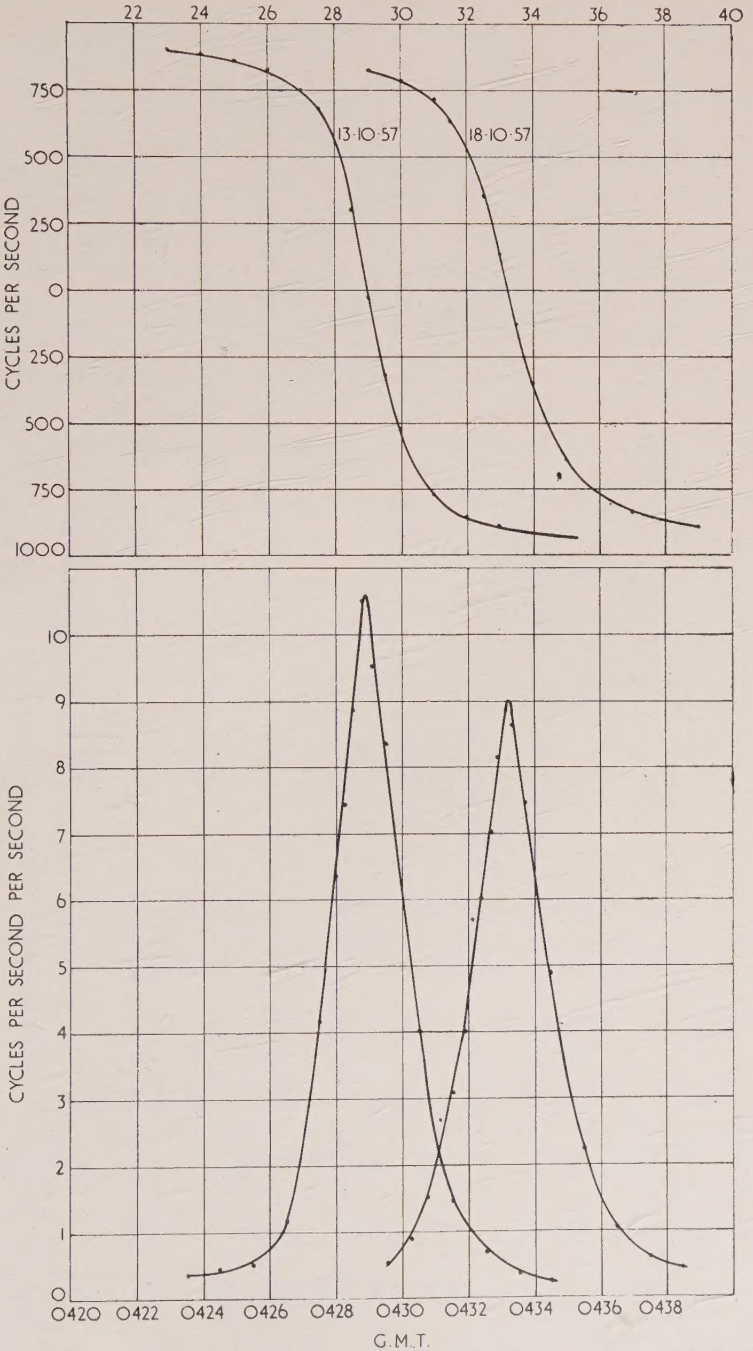

FIG. 1.—Observations on similar transits of Sputnik I on two successive days, 18 and 19 October 1957. The upper curves show the frequency shift; the lower curves show the rate of change of frequency shift for the two transits.

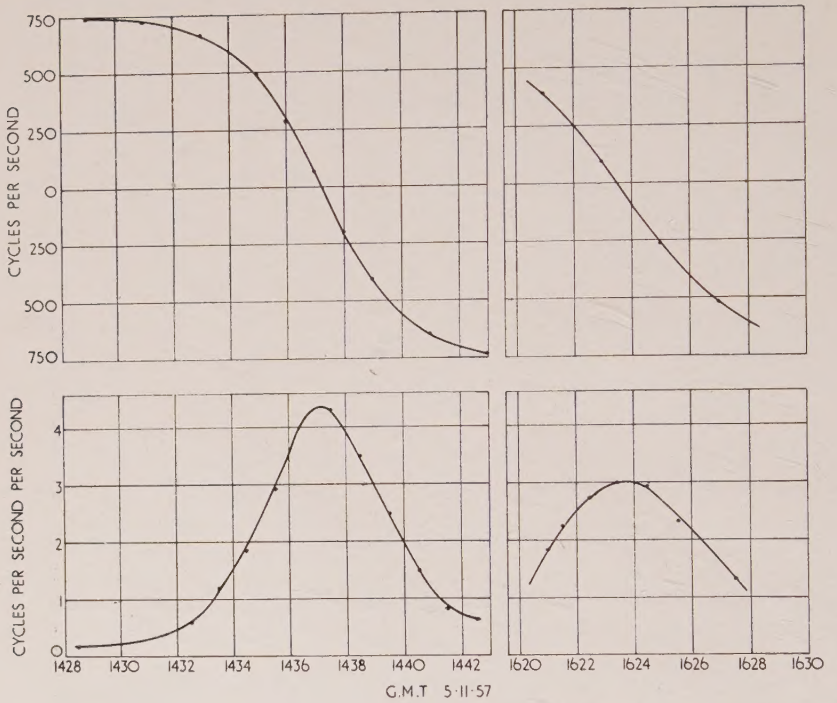

FIG. 2.—Observations on successive transits of Sputnik II on 5 November 1957. The upper curves show the frequency shift; the lower curves show the rate of change of frequency shift for each transit.

that sufficient accuracy was obtained from fairly simple apparatus. The following sections describe how the measurements were interpreted.

THE DOPPLER SHIFT AND ITS RATE OF CHANGE

Take the observer to be at rest at a distance R from the centre of the earth as represented in Fig. 3, and suppose that the relative motion of the satellite takes it at a speed V on a circular orbit of radius r about the centre. The satellite will not necessarily pass overhead, and one may suppose that the observer and the point at which the satellite makes its closest approach subtend an angle d at the centre of the earth.

At a time t after making its closest approach, the satellite has moved through an angle Vt/r around its orbit. The observer and the satellite now subtend at the centre an angle θ which is the hypotenuse of a right-angled spherical triangle, and

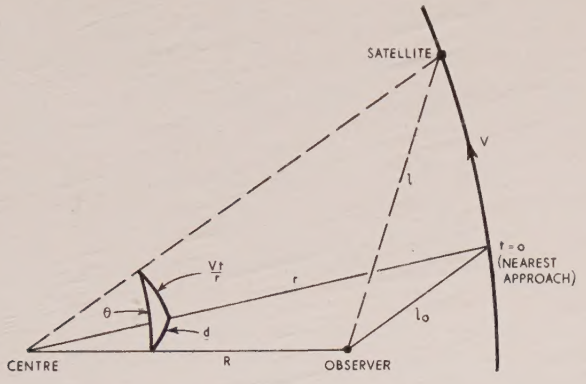

FIG. 3.—Geometry of the transit of a satellite past a stationary observer.

$$\cos\theta = \cos d.\cos Vt/r$$

The distance l between the satellite and the observer is given by

$$l^2 = r^2 + R^2 - 2rR\cos\theta$$

$$= r^2 + R^2 - 2rR\cos d.\cos Vt/r$$

Since the radio wavelength at frequency f is c/f (c = the velocity of light), the Doppler decrease in frequency is

$$D = f/c\ .\ \partial l/\partial t = f/c\ .\ RV/l\ .\cos d.\sin Vt/r$$

The rate of change of Doppler shift is greatest at zero time when the satellite makes its closest approach, l_0. The value of this maximum

$$\left(\frac{\partial D}{\partial t}\right)_{\max} = \frac{fRV^2}{crl_0}\ .\cos d \qquad \text{..... (1)}$$

The slant distance l_0 is estimated from this formula.

A further refinement for an orbit of small eccentricity e, and semi-major axis a, is to treat it as a circle whose radius is a and whose centre is displaced a distance ae from the centre of the earth. The maximum rate of change of Doppler shift is then

$$\left(\frac{\partial D}{\partial t}\right)_{\max} = \frac{fV'^2}{cl_0} \frac{R \cos \dot{a} + a - r}{a} \qquad \text{..... (2)}$$

where r is the radius at the point of observation and V' the relative velocity between the satellite at this point of its orbit and the observer rotating with the earth (see equation 6).

ESTIMATING THE ORBIT

If the satellite is moving in a plane which intersects the earth's surface in a great circle such as is shown as a broken line in Fig. 4, an observer who moves with the rotation of the earth along some line of latitude (colatitude θ) may observe transits of the satellite when he is near the plane of its orbit. Let t and t' be the instants at which the satellite approaches the observer most closely in its south-going passages that occur just before and just after he crosses the plane of the orbit. At these instants the observer will be at ascertainable positions on his path, as indicated in Fig. 4. Similarly, the satellite when going north may make its nearest approaches on the east and on the west at times s and s'. From the times t and t' it is possible to make a rough estimate of the time T at which the observer passes through the plane of the orbit; that transit in which the rate of change of frequency is least is the one in which the observer is farthest from the orbit. Similarly, it is possible to estimate the time S at which the observer passes through the orbital plane where the satellite moves north.

Times T measured on successive days (say, T_1, T_2) will not necessarily be at an interval of exactly 24 hours (sidereal time). Any difference shows that the orbital plane is rotating slowly about the earth's axis. For the purpose of predicting sightings, however, it is necessary to note by how much the instant T, measured in solar time, changes from day to day.

The inclination of the orbital plane to the earth's axis can be estimated. Thus, the angle ϕ shown in Fig. 4 is

$$\phi = \frac{180\ (S - T)}{T_2 - T_1} \text{ degrees}$$

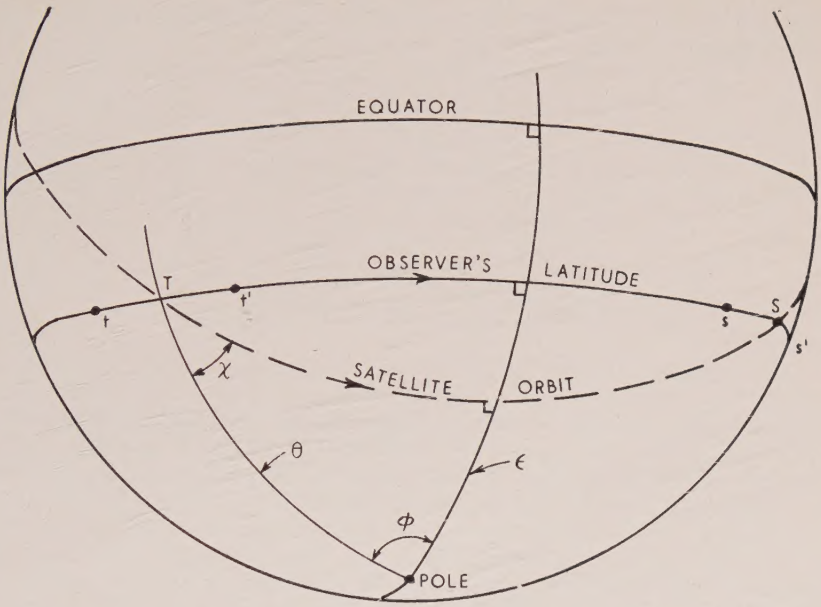

FIG. 4.—The plane of the satellite orbit cuts the earth's surface in a great circle (broken line) and the earth rotates, carrying the observer along a line of latitude. He passes through the plane of the orbit at positions T and S, but transits of the satellite will in general occur before or after he passes the plane—say, when he is at t and t' or s and s'. (These symbols are also used to denote the times of these events.)

Then, from the spherical triangle, the inclination ϵ between the plane of the orbit and the axis of the earth is given by

$$\tan \epsilon = \cos \phi \, . \, \tan \theta \qquad \ldots\ldots\ldots (3)$$

The direction in which the satellite will appear to move is determined principally by the angle χ between the orbit and the observer's north-south line. This is given by

$$\tan \chi = \cos \phi \, . \, \sec \theta \qquad \ldots\ldots\ldots (4)$$

However, the motion of the observer makes the relative direction slightly different. It is, to a sufficient accuracy,

$$\chi' = \chi - \frac{\tau}{24} \sin \theta \, . \, \cos \chi, \text{ radians} \qquad \ldots\ldots\ldots (5)$$

where τ is the orbital period (in hours). The apparent velocity V' is (in distance per hour)

$$V' = V - \frac{2\pi R}{24} \cdot \sin\theta \cdot \sin\chi \qquad \ldots\ldots\ldots (6)$$

OTHER CHARACTERS OF THE ORBIT

The geometry of the orbit in the vicinity of point T or point S (Fig. 4) is pictured in Figs 5 and 6. Figure 5 is a projection on a vertical plane through T, at right-angles to the plane of the orbit. The orbit appears as the point A. The observer's path tTt' is along a line of latitude, not in the plane of the diagram. The path therefore appears foreshortened in this diagram by the factor cos χ. Figure 6 is a plan projection in which great circles appear as straight lines. The curve tTt' is the line of latitude along which the observer moves, and in this projection it has a radius R tan ϕ. At the times of closest approach, the observer is at t or t' and the satellite is at A or A'. The perpendictular distances from the points t and t' to the plane of the orbit are shown as d and d'.

These constructions assist the calculation, which is a process of successive approximations. Thus, in the time $t' - t$ between the two successive transits, the observer is carried a distance k towards the east, where

$$k = \frac{t' - t}{T_2 - T_1} \cdot 2\pi R \sin\theta \qquad \ldots\ldots\ldots (7)$$

In Fig. 5 the distance tt' is k cos χ. We estimate the slant distances l and l' (between the observer and the satellite at the times of nearest approach) from the Doppler measurements, using equation (1), but to do this it is necessary to adopt some plausible values for d and d' (say, $\frac{1}{2}k$ cos X), and for r and for V; r and V are connected with the measured period τ by the two standard orbit formulae (Smart, 1940), in which G is the gravitational constant and M is the mass of of the earth.

$$a^3 = GM\,\tau^2/4\pi^2 \qquad \ldots\ldots\ldots (8)$$

$$V^2 = GM\,(2/r - 1/a) \qquad \ldots\ldots\ldots (9$$

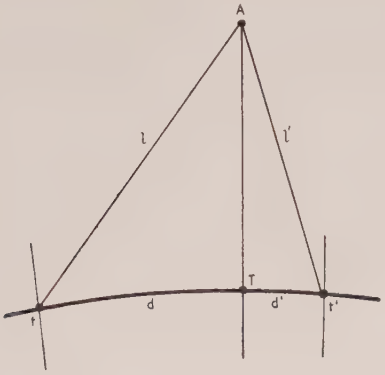

FIG. 5.—A projection of the observer and satellite on a plane normal to the orbit. Transits occur when the observer is at t and t' The slant distances to the orbit A are l and l'. These are not sensibly different from distances of nearest approach of the satellite. The track tTt' is drawn with the earth's radius (R). The construction is used to find values of d, d', r, and V.

For a first trial, one may assume the radial distance r to be equal to the semi-major axis a. The figure constructed with these values of l and l' gives improved values of d, d', and r. Using these new values in equations (9) and (2), we get improved values of l and l' for a second construction. Repeating the process quickly gives self-consistent values for the height and velocity of the satellite and for the time T at which the observer passes through the orbital plane.

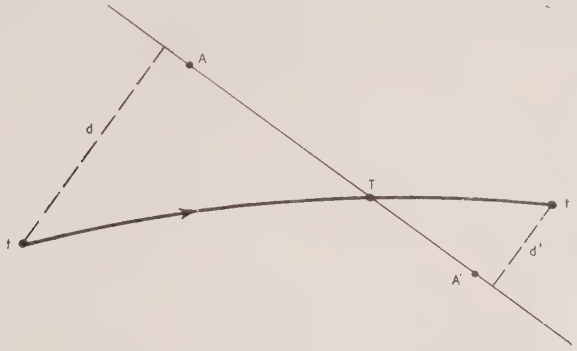

FIG. 6.—A plan projection of the observer and satellite that presents great circles as straight lines. The observer's path is the latitude line tTt' and the satellite's path is the great circle ATA'

In Fig. 6, the interval tTt' is an arc of radius $R \tan \theta$ and its length is k (equation 7). The perpendicular distances d and d' are known from Fig. 5, and they are used to construct the projection of the orbit AA'.

The purpose of this construction is to measure AT and TA' and thence to find out when the satellite crosses the latitude line, these times being a few minutes before or after the instants at which the satellite makes its nearest approach. The period of the satellite may be calculated more exactly from these times.

PREDICTING FUTURE TRANSITS

The interval $t' - t$ in Fig. 4 is an approximate measure of the orbital period. It is an overestimate when the satellite rotates about the earth's axis in the same sense as the earth itself. For Sputniks I and II, the excess was about three minutes.

This approximate measure of the period is used to determine what integral number of rotations will occur between the times of two similar transits made on successive days. These then give a more accurate measure of the orbital period.

The period must be calculated from the times of transit of the satellite across the observer's latitude line. The previous section has shown how these times can be estimated from the times and distances of nearest approach. From observations made on successive days, the period can be found to the nearest second (0·02 min.).

When Sputnik I was first set in orbit, the periodic time was announced to be 96·2 min. Our radio observations began a fortnight later, and on 18 October the period was found to be 95·70 min. Thereafter it decreased at an almost uniform rate of 2·3 sec. per day until the last radio measurements, on 25 October, gave the period as 94·4 min. Fourteen days later the satellite was seen in transit, and the observed time was within a minute of the time predicted from the radio observations.

In the case of Sputnik II, radio observations were made between 5 November and 8 November, and they enabled the following details to be deduced about the satellite orbit as it was at about 11 hr (U.T.) on 5 November 1957.

DETAILS OF SPUTNIK II ORBIT DERIVED FROM DOPPLER SHIFT MEASUREMENT

Time of transit of latitude 41·3° S while travelling south	5/11/57 10 h 41·1 m U.T.
Longitude of the above transit	124° W
Time of transit of latitude 41·3° S while travelling north	5/11/57 11 h 11·2 m U.T.
Longitude of the above transit	254° W
Theoretical precession rate	26·12° W/rev
Period	103·66 min.
Rate of decrease of period	0·0037 m/rev
Height going south	1160 km
Height going north	1080 km

CONCLUSIONS

The apparatus for the measurement of the Doppler change in frequency is fairly simple and has given good results. The method of analysis that has been described is not too lengthy, and it has been successful in defining the time and the direction at which the satellite should be sought, as far ahead as a fortnight after the end of the radio observations.

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SULPHUR ISOTOPIC VARIATIONS IN NATURE

PART 6—SULPHUR ISOTOPIC MEASUREMENTS ON THE DISCHARGE FROM FUMAROLES ON WHITE ISLAND

By T. A. RAFTER, Division of Nuclear Sciences, S. H. WILSON, Dominion Laboratory, and W. B. SHILTON, Division of Nuclear Sciences, Department of Scientific and Industrial Research, Wellington.

(Received for publication, 11 February 1958)

Summary

A method has been developed for sampling the discharge gases from fumaroles on the volcano, White Island. Forms of sulphur other than free sulphur and sulphate have been identified. Initially, sulphate forms a very small part of the total sulphur in the discharge. The ^{34}S enrichment values for the sulphur, as free sulphur and as total soluble sulphur, have been measured for six fumaroles. The percentage of each form of sulphur was determined quantitatively and an overall $^{32}S/^{34}S$ ratio of 22·15 calculated for these fumaroles. This value indicates that the sulphur in the parent magma is of igneous origin. The so-called "volcanic sulphur" appears to be enriched in ^{32}S by chemical reactions at the vent mouth. The wide spread of isotopic values for sulphate found, means that little significance can be placed on sulphate isotopic values around volcanic areas. The necessity for careful sampling of the discharge is emphasized before basic information can be obtained as to the origin of volcanic sulphur.

If sulphur from volcanic exhalations can be shown generally to have an average sulphur isotopic ratio similar to that of sulphur in the igneous rocks, then these additions of sulphur to the ocean cannot account for the present enrichment of the heavy isotope of sulphur in ocean sulphate.

INTRODUCTION

On White Island, an active andesitic volcano in the Bay of Plenty, there are a number of large fumaroles within the crater, emitting steam laden with hydrochloric acid and sulphur gases. Temperatures of 500° C or more have been measured in some of these fumarole discharges. Sulphur can actually be seen distilling from the vents. The magma is presumably close to the surface at White Island. A study of the sulphur isotopic ratio in fumarole discharge was undertaken to determine, if possible, the origin of sulphur in these exhalations.

Macnamara and Thode (1950) suggested that the abundance of isotopes of sulphur in troilite, extracted from meteorites, should represent the primeval sulphur isotopic ratio and could be considered as the base level to which all terrestrial sulphur isotopic fractionation, shown to exist, could be compared. The very narrow spread in the abundances of the sulphur isotopes for nine meteorites (average $^{32}S/^{34}S = 22·14$) supported this conclusion. Macnamara, *et al.* (1952) studied the sulphur isotopic abundances in igneous rocks and sulphide

ores of igneous origin. They were able to show that the average $^{32}S/^{34}S$ ratio of 22·15 agreed closely with the value found for meteoritic sulphur. Sulphide ores of igneous origin, which constitute a negligible portion of igneous sulphur, appeared to be enriched slightly in ^{34}S with respect to meteoritic sulphur. This indicated that some fractionation of the sulphur isotopes occurred as a result of the early fractionation of the sulphide minerals.

The isotopic ratio for volcanic sulphur has been reported by Lazard, *et al.* (1952) and Rankama (1954). The average $^{32}S/^{34}S$ value for seven determinations is 22·15. In a recent paper by Sakai (1957) the average value for fifteen specimens of volcanic sulphur is given as 22·20. If any chemical fractionation of the sulphur isotopes takes place at the vent of the volcano or fumarole, the isotopic ratio of volcanic sulphur which can readily be obtained around the vents would not truly represent the sulphur isotopic ratio of the parent material. If the discharge from the fumaroles on White Island could be adequately sampled so that all forms of sulphur in the discharge could be recovered and their isotopic ratio estimated, the sulphur isotopic ratio for the parent magma could be determined.

On account of the high temperature of the discharge from some of the fumaroles, special sampling techniques had to be developed. Seven fumaroles were examined, the various forms of sulphur quantitatively estimated, and from the $\delta^{34}S$ values obtained, it was possible to derive the average $^{32}S/^{34}S$ ratio for six of the fumaroles, the overall average $^{32}S/^{34}S$ ratio for the sulphur in the total discharge, and hence a closer $^{32}S/^{34}S$ value for the sulphur in the parent volcanic magma.

At the same time as the fumaroles were sampled, specimens of sulphur forming around each vent were collected and their sulphur isotopic ratio measured for comparison purposes.

DESCRIPTION OF THE FUMAROLES ON WHITE ISLAND

The fumaroles on White Island and their changes with time are described by one of the authors (Wilson, in press).

Fig. 1 shows a map of the crater at White Island on which the fumaroles have been marked. From the north end, anti-clockwise round the crater, are the following active areas:

Seven Dwarfs: Discharge Temperature 122° C

These fumaroles were fairly easily accessible for sampling, but the volume of steam was not great.

Noisy Nellie:

This consists of two large fumaroles, one above the other, in a deep pit. The lower fumarole could have been sampled, but conditions in the pit were bad unless the wind was favourable.

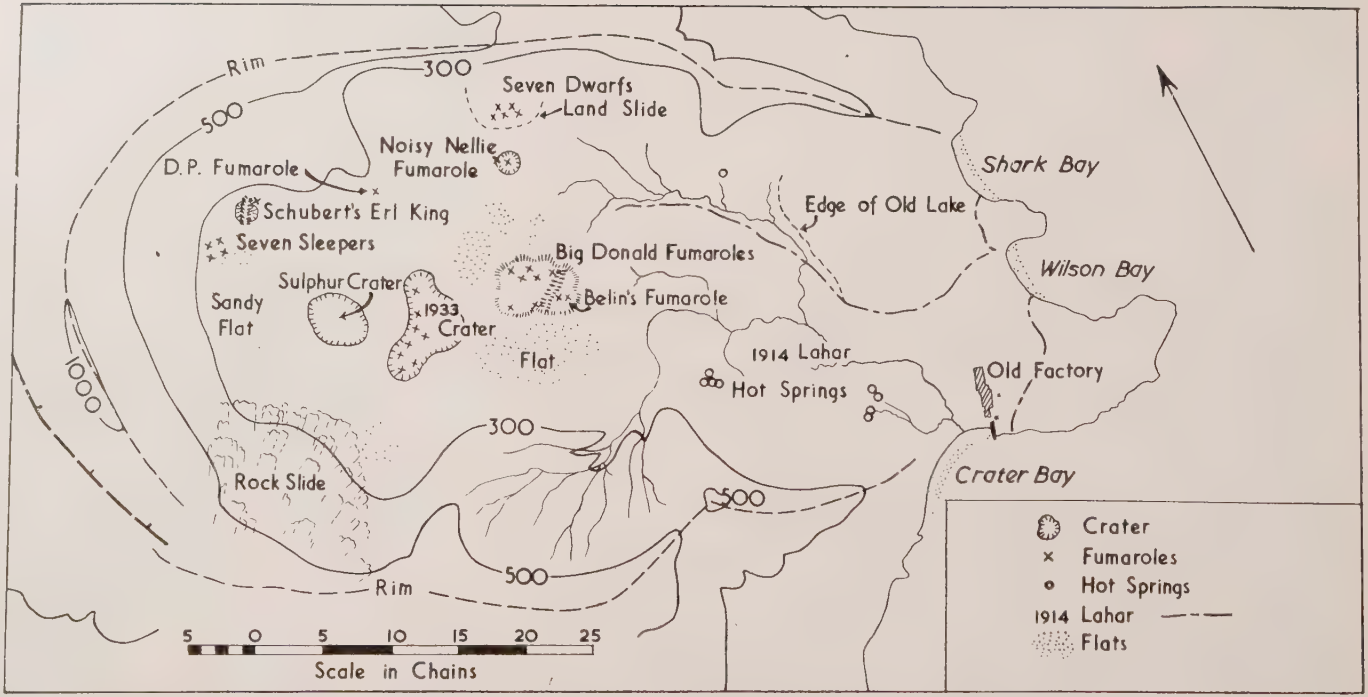

FIG. 1.—Sketch map of White Island crater showing fumaroles examined. (map after Healy, *in press*).

D.P. Fumarole: Discharge Temperature 109° C

This fumarole is noted for sputtering fairly strong hydrochloric acid.

Schubert's Erl King: Discharge Temperature 179° C

At Schubert's Erl King there were several vents, and a suitable one was found for sampling.

Seven Sleepers

A group of small fumaroles with sulphur depositing round the vents has been formed since the back of the crater was last seen by one of the authors (S. H. W.) in 1951. This was named the "Seven Sleepers". The group is not far from Schubert's Erl King and is probably similar in character.

Sulphur Crater

The high temperatures at Sulphur Crater cause the sulphur in the steam to burn to sulphur dioxide and sulphur trioxide. The former is very evident, making sampling uncomfortable. A suitable fumarole to sample might have been selected when the wind was favourable, but there was no opportunity to do this.

Fumaroles in the 1933 Crater

These have always been inaccessible.

Donald Fumaroles: Discharge Temperatures 560° to 570° C

No fumarole particularly convenient for sampling on the Big Donald mound was located.

Fumaroles on a small mound to the south-east of Big Donald Mound glowed dull red at night, and the temperature of one (Belin's Fumarole) was 580° C. This was obviously the best place of all to take a sample. In a changeable wind the fumes from this fumarole were often unbearable, but fortunately a strong favourable wind did enable thorough sampling to be done at Belin's Fumarole. Samples were also collected from a more accessible vent west of Belin's Fumarole.

EXPERIMENTAL PROCEDURE

Method used for the Sampling of Fumarole Discharge

The tubes used for drawing steam from the fumarole had to be resistant to the highest temperature expected and to acid gases. Two types of tubes were tried. The first was a silica tube 1cm diameter, about 150cm long, with a short limb of 30cm at right-angles. For protection against breakage, the tube was packed with diatomaceous earth inside an iron pipe. About 50cm of the long limb of the steel tube was separated off by rubber stoppers and provided with inlet and outlet tubes, so that this portion could be used as a condenser. The second type was a copper tube 1·0cm outside diameter, the inside of

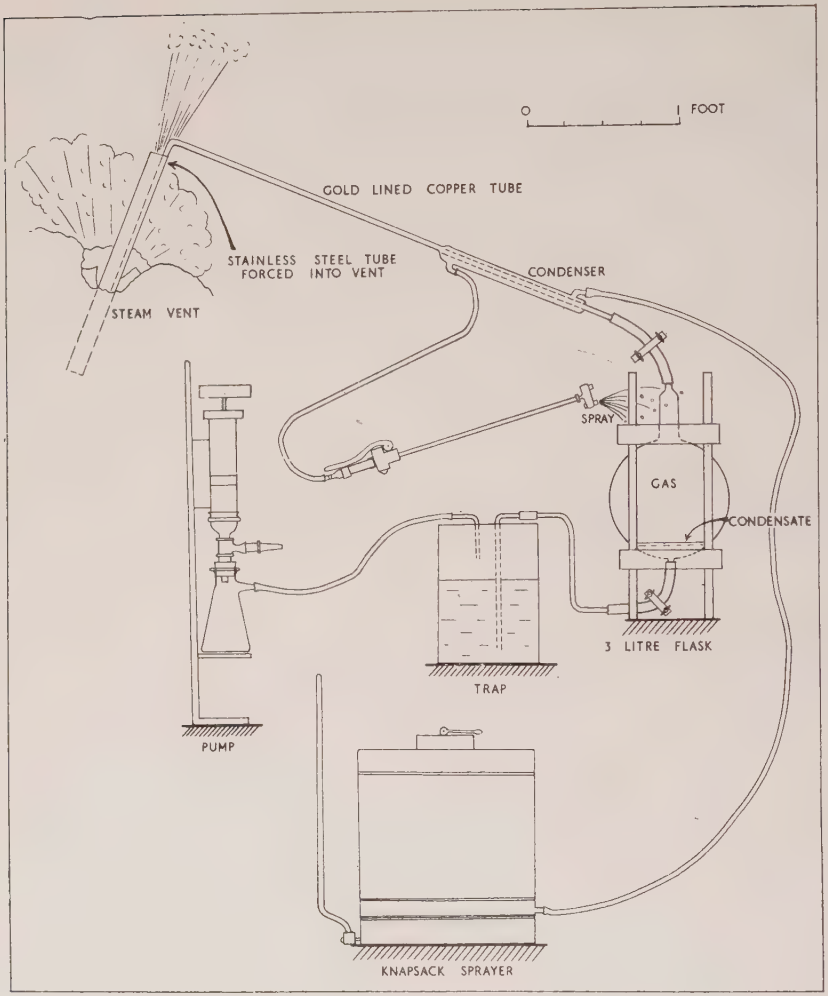

FIG. 2.—Apparatus for collecting a gas-and-condensate sample from fumaroles.

which was protected by a lining of gold (0·013cm) and the internal diameter of the tube was 0·55cm. This tubing was made into two bent tubes with short limbs of 30cm, and long limbs of 60cm and 90cm respectively. A jacket for water cooling, 45cm long, was provided on each tube. These two tubes had to be joined together with rubber tubing at the hottest fumarole to give a total length of 150cm.

The method of gas collection (Fig. 2) was a modification of that used to collect gas from bores at Wairakei and from fumaroles on the mainland (Wilson, 1955). The gas and condensate were collected

in spherical glass flasks as shown in Fig. 2. These flasks have 1cm diameter inlet and outlet tubes. Air was removed from the flasks by pumping water from the trap into the flask and up the collecting tube into the steam. Then the water was sucked out by the pump, back into the trap drawing steam into the flask and through the trap for some time to remove any air left. The screw clip on the rubber tubing on the lower end of the flask was then closed. The flask was cooled by spraying it with water from a knapsack sprayer. The water from the knapsack sprayer was taken through plastic tubing to the condenser on the silica or copper-gold tube, and then to the spraying nozzle. As long as steam was condensing in the flask, steam and gas were being drawn in, and it was possible to judge by feeling the flask when collection of gas had practically finished. Flasks were taken of capacity 5, 3, and 2 litres.

As the number of flasks was limited, some of the samples for isotope determinations were prepared on the island, although no quantitative determinations of gas were made then. About 30ml of carbonate-free 20% sodium hydroxide solution was added to a 2 litre flask, well shaken and the extract decanted from sulphur and transferred to a bottle and labelled "alkaline extract of gas and condensate". The sulphur was washed with water and kept.

Owing to the large amount of gas in the steam, and the narrow bore of the sampling tube, it was impossible to collect condensate directly into a bottle as the tube blocked with cold gas. It was necessary to collect a sample of gas and condensate in one of the flasks, and then pour the condensate into a sample bottle. It was hoped to use samples of condensate for the determination of the concentration of sulphuric acid in the steam, and for the isotope ratio of the sulphur in it. It was proposed immediately after collection, to pass a stream of gas through the condensate to remove hydrogen sulphide, and sulphur dioxide. For this purpose, a cylinder of carbon dioxide was taken to the island. Unfortunately, in transport the valve was knocked and the cylinder was found to be empty. Hence, it was necessary to use acetylene because a cylinder of this gas had been taken for use, if required, to seal glass tubing. It appeared, however, that even though the volatile sulphur compounds were removed as soon after collection as possible, there had yet been time for polythionates to form, so that the sulphur still left in combination in the condensate was not solely in the form of sulphate.

At most of the fumaroles, there were sulphur deposits round the vent. Samples of these were also collected for sulphur isotope determination.

Quantitative Chemical Analysis

Samples of gas and condensate in 5-, 3-, and 2-litre flasks were brought back to Wellington. As these samples were required for the determination of total gas content of the steam, of carbon dioxide

and other gases, as well as the sulphur gases, the preliminary analysis was made in the Dominion Laboratory. The presence of sulphur, together with hydrogen sulphide, and sulphur dioxide, very greatly complicated the analysis. The method used, with the sample flasks of the steam of Wairakei bore discharges, is to remove carbon dioxide and hydrogen sulphide by adding sodium hydroxide solution. With the White Island samples, this was undesirable, owing to the possible action of strongly alkaline solution on sulphur and polythionic acids. For this reason, the method adopted was to remove the condensate from the gas by drawing the condensate into an evacuated Dreschler bottle. Water was then added to the flask in several portions and removed in the same way to wash out all the sulphur. The water also removed from the gas phase all the sulphur dioxide and most of the hydrogen sulphide. A solution of 20% sodium hydroxide was then added to the gas in the flask to remove carbon dioxide and the remainder of the hydrogen sulphide. This extract was transferred to a stoppered measuring cylinder and labelled "alkaline extract of the gas".

The sulphur was removed from the condensate and washings during transfer to the Dreschler bottle, by means of a glass sinter filter between the flask and the bottle. The condensate and washings ("diluted condensate") were kept in these Dreschler bottles under nitrogen. Hydrogen sulphide and sulphur dioxide were determined in a portion of the "diluted condensate" by titration with iodine after adjusting the pH to 5. Sulphur dioxide could be estimated by titrating again with sodium hydroxide solution after the iodine titration. The extra amount of acid formed when sulphur dioxide was present permitted the amount of sulphur dioxide to be calculated.

From another portion of the "diluted condensate", the sulphur dioxide and hydrogen sulphide were removed by passing a current of nitrogen through the solution. Sulphuric acid was then determined in this solution by precipitation with barium chloride. Unfortunately, it was not realized at the time that so large a proportion of the sulphur was present as polythionic acids, and the sulphate obtained was largely formed from decomposition of the polythionic acids when the solution was heated during the precipitation.

Hydrogen sulphide was also determined in a portion of the "alkaline extract of gas" by titration with iodine in 20% sodium hydroxide solution (Frost, 1944). The amount of sulphur dioxide in this was negligible owing to the much greater solubility of sulphur dioxide in the water washings.

In order to prepare solutions containing all the sulphur compounds for the isotope work, the "diluted condensate" and the "alkaline extract of the gas" were combined in the correct proportions and labelled "reconstituted solution". Unfortunately, polythionic acids are decomposed in alkaline solutions and as the combined solution was strongly alkaline, it was not possible to determine the polythionic acids later, when the large amount present was realized. The polythionic acids

are formed from the chemical action between hydrogen sulphide and sulphur dioxide in the samples after collection. If polythionic acid had been determined it would have been possible to calculate the original content of hydrogen sulphide and sulphur dioxide in the gas. As it is, the content of sulphur dioxide and hydrogen sulphide originally in the gas was underestimated in the original analysis, and the best determination of the concentration of the sulphur gases in the condensate was from the determination of total "soluble-sulphur" carried out in the isotope work.

It is now realized from the small amount of hydrogen sulphide in the "alkaline extract of the gas", that the better method would have been to continue the washings with water till practically all the hydrogen sulphide was removed from the gas phase. The "alkaline extract of the gas" would then have been required only for the determination of carbon dioxide not removed with water, and it would not have been necessary to mix the "diluted condensate" with the "alkaline extract of the gas".

Chemical Procedures for Sulphur Isotopic Examination

On account of the difficulties experienced in the examination of the compounds of sulphur in geothermal bore waters (Rafter, *et al.*, 1958), when the specimens from White Island were analysed, particular care was taken to recover not only sulphur and sulphate but also what has been called "soluble-sulphur". This is a very stable sulphur compound, probably a polythionate, that does not precipitate with the sulphate on the addition of $BaCl_2$, but is recovered from the filtrate (after removal of sulphate as $BaSO_4$) by oxidation with bromine and precipitation as a second $BaSO_4$ precipitate.

A variety of specimens and solutions were received for recovery of sulphur for isotopic examination and were examined in the following manner.

(1) Condensates with H_2S and SO_2 removed by a stream of gas at White Island

As explained above, soon after collection, the condensate was swept with acetylene gas in an attempt to remove volatile sulphur gas, leaving only sulphate for isotopic examination. When these solutions were received a large amount of sulphur had separated out. This was removed by filtration and purified by solution in hot benzene. The clear filtrate was usually tested for the presence of sulphide, but in **no** case could an Ag_2S precipitate be obtained on the addition of $AgNO_3$. A portion of the solution was tested with iodine solution and if an iodine titre was obtained, sulphate and sulphite were precipitated by the addition of $BaCl_2$ in the cold, warming the precipitate and allowing to stand overnight. The sulphite was separated from the sulphate after filtration by digestion with 1:2 HCl, the sulphur dioxide evolved being oxidized by iodine to sulphate. After the removal of sulphite and sulphate, the filtrate was examined for "soluble-sulphur" by

TABLE 1.—Sulphur Isotope Enrichment of Various Forms of Sulphur in the Discharge from White Island Fumaroles.

Fumarole	Discharge Temp. (° C)	Sample No.	Dom. Lab. Ref.	Specimen	$\delta^{34}S$ Enrichment with respect to sea-water sulphate: Sulphur $\delta^{34}S$ (‰)	Sulphate $\delta^{34}S$ (‰)	Sulphite $\delta^{34}S$ (‰)	"Soluble-sulphur" $\delta^{34}S$ (‰)	Total soluble sulphur $\delta^{34}S$ (‰)	Wgt. ratio SO_4= to total soluble sulphur
Belin's Donald Mound	570	R107	C/96/2	Condensate with H_2S and SO_2 removed	−24·1	− 6·0	—	−18·8	−12·0	1/10
		R111	ae 2	Alkaline extract of gas and condensate					−12·0	—
		R115	S51	Sulphur above vent	−19·8					
		R130/132	gcf 16/1	Condensate	−20·8	−10·2			−19·8	4/10
Vent under rock south of gully through Donald Mound	562	R110	ae 1	Alkaline extract of gas and condensate		−12·8	−19·4	−18·6	−12·8	1/3
		R114	S50	Sulphur separated from R110	−23·6					
		R113	S49	Sulphur above the vent	−22·2					
		R143/4/5	gcf 20	Condensate — S — SO_4=	−26·4	− 1·3			−16·8	
Schubert's Erl King	179	R112	ae 3	Condensate and Sulphur	−26·2				−17·2	
		R117	S53	Sulphur around vent	−23·8					
		R124/133/134A	gcf 17/1a	Condensate — S — SO_4=	−22·0	− 5·5			−13·7	1/1
		R135/137	gcf 17/1b	Condensate — S — SO_4=	−22·5	− 6·8			−11·7	2/25

Seven Sleepers		R109	C/100/2	Condensate with H_2S and SO_2 removed	—	+ 0·2		— 12·7		
		R140	gcf/19	Condensate — S — SO_4=	— 26·5	— 9·5			— 14·2	1/8
D.P. Fumarole	109	R118	S54	Sulphur around vent	— 23·6	— 2·8				
		R123	gcf/15	Condensate — S — SO_4=	— 23·3	— 9·4			— 11·0	
Seven Dwarfs	122	R119	S55	Sulphur around vent	— 22·8					
		R108	C/99/2	Condensate with H_2S and SO_2 removed	— 22·9	— 4·4		— 13·0		1/1
		R138/139	gcf/18	Condensate — S — SO_4=	— 24·4	— 4·3		n.a.		
				Average	— 23·4				— 14·1	

bromine oxidation. In addition, total "soluble-sulphur" was recovered by bromine oxidation before the sulphate precipitation in a separate aliquot.

(2) Sulphur collected from around the vent

This sulphur, before isotopic examination, was purified by solution in benzene, filtering the benzene extract through a No. 41 Whatman filter paper into a platinum basin, and evaporating off the benzene on a water-bath.

(3) "Alkaline extract of gas and condensate"—White Island

These alkaline extracts prepared on White Island should contain all the sulphide, sulphite, sulphate, and "soluble-sulphur" in the fumarole discharge. The sulphur that precipitated out of these extracts on collection had been removed by decantation by one of the authors (S. H. W.) and sent in separately, from the clear filtrate. These extracts were simply oxidized with bromine to recover total "soluble-sulphur". However, as shown in Table 1, one of these extracts, R.110, was analysed for sulphate, sulphite, "soluble-sulphur", and total soluble-sulphur.

(4) Condensates

The condensates listed in Table 1 refer to the "reconstituted solution", for isotopic examination from the "alkaline extract of the gas" and the "diluted condensate" as explained under quantitative chemical analysis. From these condensates total soluble-sulphur only was recovered.

The sulphur recovered during the separation of the "diluted condensate" from the gas phase and the sulphate recovered as $BaSO_4$ were simply tested for purity before isotopic examination.

The sulphur in the barium sulphate precipitates was converted to sulphur dioxide for mass spectrometer examination by the method described by Rafter (1957).

RESULTS

In Table 1 the enrichment values ($\delta^{34}S$) for the $^{34}S/^{32}S$ ratio of specimens with respect to the sea-water sulphate-sulphur standard have been expressed as ‰ (per mil) for each form of sulphur recovered. Whenever possible, the various forms of sulphur were recovered quantitatively so that the average isotopic ratio for the sulphur in fumarole discharge could be calculated as shown in Table 2.

Using the $\delta^{34}S$ enrichment values from Table 1 for insoluble sulphur in the discharge and for sulphur collected from around the vents of each fumarole, an average $\delta^{34}S$ value for insoluble sulphur was calculated for each fumarole and recorded in Table 2, Column 7. In a similar way the average $\delta^{34}S$ value for soluble-sulphur was calculated as shown in column 10, Table 2. Knowing the millimols of insoluble and total soluble-sulphur in the discharge from each fumarole, overall $\delta^{34}S$ values have been calculated and recorded in column 15.

DISCUSSION

The $\delta^{34}S$ values for sulphur around the vents of the fumaroles and that precipitated out of the discharge both during and after collection, are the same within the limits of the mass spectrometer measurements. The sulphate $\delta^{34}S$ values (Table 1) show a wide spread, as is to be expected. This sulphate is not entirely the sulphate issuing at the time of collection, but some of it had been subsequently formed by the oxidation of polythionates or sulphite either present in the discharge or formed during collection. The sulphate $\delta^{34}S$ values, particularly where an attempt had been made to remove all volatile sulphur gases, show a considerable depletion in the lighter sulphur isotope with respect to the sulphur in the discharge.

The sulphite and polythionates existing in solution at the same time as the sulphate are definitely enriched in the lighter sulphur isotope with respect to sulphate-sulphur. Since the sulphate existing in the total discharge, as shown in the last column of Table 1, can amount to as little as 8% of the total soluble-sulphur, it is obvious that to obtain the true value for the sulphur isotope ratio of fumarole discharge, total soluble-sulphur, not sulphate-sulphur, must be examined. The large amounts of polythionates existing in these condensates is a significant observation.

The sulphur dioxide in the original steam will react with hydrogen sulphide to give polythionates according to the general formula

$$a\,H_2O + b\,H_2S + c\,SO_2 \rightarrow d\,H_2\,S_x\,O_6$$

Other reactions through the introduction of any air during collection would be the oxidation of H_2SO_3 to H_2SO_4, and of H_2S to sulphur. The sulphur recovered by filtration will thus contain not only the sulphur originally in the steam but that also formed chemically by various oxidation-reduction reactions.

The average $\delta^{34}S$ isotopic enrichment value for the sulphur collected around the vent, as shown in Table 2, is $-22{\cdot}2‰$ with respect to the sea-water sulphate standard, while that for sulphur separated from the condensates is $-23{\cdot}9‰$. Thirteen additional sulphur specimens collected in the same area and reported by Rafter (in preparation) gave an average $\delta^{34}S$ value of $-26{\cdot}6‰$. It can be observed at White Island that sulphur distills out of the fumarole vent. This sulphur and that formed by chemical reactions at the vent mouth are isotopically not significantly different.

No attempt has yet been made to carry out an extensive survey of the various forms of sulphur existing in fumarole condensates. Specimen R.107 was examined several months after collection. After removal of sulphur by filtration, the clear filtrate was found to contain sulphate, trithionate, and tetrathionate in the ratio, by weight, of 1:1:2. Sulphite, thiosulphate, and pentathionate were not present.

TABLE 2.—Quantitative Estimations for Soluble and Insoluble Sulphur in Fum- Enrichment with respect to

	1	2	3	4	5	6	7
Fumarole	Lab. No.	Dom. Lab. No.	Insoluble S (milli-mole)	Total soluble S (milli-mole)	Volcanic S $\delta^{34}S$ (‰)	Insoluble S $\delta^{34}S$ (‰)	Insoluble (average) S $\delta^{34}S$ (‰)
Belin's Donald Mound	R130 132 107 111 115	gcf/16	3·18	6·56	—19·8	—20·8	—20·3
Vent south of Donald Mound	R110 113 143 144 145	gcf/20	8·39	12·79	—22·2	Wn. —26·4 W.I. —23·6	—24·1
Schubert's Erl King	R124 133 134A 117 112	gcf/17/1a	10·92	22·10	—23·8	Wn. —22·0 W.I. —26·2	—24·0
	135 136 137	gcf/17/1b	16·76	32·10	—	—22·5	—22·5
Seven Sleepers	R140	gcf/19	10·48	29·5	—	—26·5	—26·5
D.P. Fumarole	R123 R118	gcf/15	5·30	6·36	—23·6	—23·3	—24·5
Seven Dwarfs	R119 108 R138 139	gcf/18	31·5	n.d.	—22·8	Wn. —24·4 W.I. —22·9	—23·6
				Average	—22·2	—23·9	—23·6

The average $\delta^{34}S$ value for "soluble-sulphur" in these discharges is significantly different from the sulphur, and both forms differ significantly from the mean overall average for White Island fumaroles (— 17·2‰). This is in accordance with the anticipated fractionation of the sulphur isotopes in chemical exchange processes. Thode, *et al.* (1949) have shown that the heavier isotopes of sulphur, particularly ^{34}S, should favour the higher valency states in the order $S^{=}$, $SO_3^{=}$, $SO_4^{=}$. Partition function ratios have not been calculated for the polythionate ions, but polythionate-sulphur should theoretically be enriched in ^{32}S with respect to sulphate-sulphur. The $\delta^{34}S$ values for "soluble-sulphur" shown in Table 1 support this prediction.

arole Discharge, their $\delta^{34}S$ Sulphur Isotopic Enrichment, and the Average Sea-Water Sulphate Standard.

8	9	10	11	12	13	14	15	16
Total soluble sulphur separated Wgtn. $\delta^{34}S$ (‰)	White Is. $\delta^{34}S$ (‰)	Soluble S (average) $\delta^{34}S$ (‰)	Product of columns 3 & 7	Product of columns 4 & 10	Sum of columns 11 & 12	Total sulphur (milli-mole)	Average fumarole $\delta^{34}S$ (‰)	$\frac{^{32}S}{^{34}S}$
—19·8	— 12·0	- 15·9	— 64·5	— 104·3	- 168·8	9·74	— 17·3	22·15
— 16·8	— 12·8	14·8	— 202·2	- 189·3	— 391·5	21·18	— 18·5	22·18
— 13·7	17·2	- 15·5	— 262·1	342·5	604·6	33·02	— 18·3	22·17
— 11·7	—	— 11·7	— 377·1	— 375·6	— 752·7	48·86	— 15·4	22·11
— 14·2	— 12·7	— 13·5	— 277·7	— 398·2	— 675·9	39·98	— 16·9	22·14
— 11·0	—	— 11·0	— 129·8	— 70·1	— 199·9	11·66	— 17·1	22·15
n.d.								
	Average	— 13·7				Average	— 17·2	22·15

Unfortunately, no sulphide-sulphur could be recovered for sulphur isotopic examination. If, as discussed by Sakai (1957), native sulphur from volcanic fumaroles is deposited through the interaction of two parts of H_2S and one part of SO_2 so that the isotopic ratio of the deposited sulphur is the weighed mean of these two gases, the H_2S should be depleted still further in the ^{34}S isotope than reported in Table 1 for native sulphur. Sakai makes no mention of other forms of sulphur other than H_2S, native sulphur, SO_2, and sulphate in the fumaroles he examined. Until rapid methods are developed for the quantitative estimation and isolation of all the various forms of sulphur, immediately after or during collection of the discharge, it would

seem to be better to consider the overall average for sulphur from fumarole discharge. The average $\delta^{34}S$ value of $-17{\cdot}2‰$ (column 15, Table 2) should be close to the true value for magmatic sulphur.

In the last column of Table 2 the $^{32}S/^{34}S$ ratio has been recorded for each fumarole. These values are very consistent within themselves. The overall average 22·15 agrees with the average $^{32}S/^{34}S$ ratio reported for six samples of sulphur from igneous rocks, by Macnamara, *et al.* (1952).

No attempt has been made to correlate fumarole discharge temperatures with isotopic fractionation factors on account of the uncertain origin of each form of sulphur identified. As shown in Table 1, three classes of sulphur of significantly different isotopic characteristics have been identified—volcanic sulphur, "soluble-sulphur" other than sulphate and sulphate-sulphur, that increase in enrichment in the heavier isotope of sulphur, in this order. Sulphate-sulphur is definitely of two classes, i.e., primary sulphate that existed in the fumarole discharge at the moment of collection and is represented isotopically by the values recorded in Table 1 for sulphate from "condensate with H_2S and SO_2 removed", the average $\delta^{34}S$ value for three determinations being $-3{\cdot}4‰$ (slightly enriched with respect to sea-water sulphate); the remainder of the sulphate must be considered as secondary sulphate formed by the subsequent oxidation of sulphites and polythionates. This sulphate can have a wide range of intermediate $\delta^{34}S$ values. No geochemical significance can be given to these intermediate $\delta^{34}S$ values except that they must be included in the overall average to obtain the isotopic value for the parent sulphur material.

Sakai (1957) reviewed the available evidence to explain the origin of heavy sulphate in the ocean. Thode, *et al.* (1953) presented evidence suggesting that bacterial activity was the most effective agency in the concentration of the heavy isotopes in the oceanic sulphate. Sakai states that Rankama and Sahama (1947) estimated that only some 35% of the present oceanic sulphate has been supplied by the weathering of igneous rocks. A part of the remaining sulphur may be a relic from volcanic sulphur compounds in the primordial atmosphere. A considerable part is, however, considered to be supplied by the degassing of the globe, throughout the geologic history of the ocean. These estimations indicate that hydrogen sulphide and sulphur dioxide exhalted during igneous activity have been playing an important part in bringing the sea-water sulphate to the present isotopic ratio.

Sakai contends that the mean isotopic ratio in hydrogen sulphide degassed out of the globe must be similar to that of the meteoritic sulphur, regardless of the degassing temperature. The range of the isotopic ratio in the sulphur dioxide on the other hand, might have undergone a significant variation, depending on the degassing temperature as well as escaping conditions from the ground surface. Sakai quotes the case of the sulphate waters of "Yugama"—the crater lake of Mt Shirane. The isotopic ratio of the sulphate ions in this lake-water is nearly equal to that in present oceanic sulphate. These sulphate

ions have been formed from sulphur dioxide evolved through volcanic exhalation. Such evidence could be interpreted as suggesting that the present ocean sulphate is the result of a contribution of exhalated sulphur dioxide of isotopic ratio equal to that of the sulphate ions in "Yugama", and secondary sulphate of isotopic ratio equal to that of meteoritic sulphur in the ratio of 65 parts of SO_2 to 35 parts of secondary sulphate.

Sakai considers also the contrary hypothesis that most of the sulphur continuously supplied to the ocean has the isotopic ratio of meteoritic sulphur. This could have occurred in two ways. It may be that, as at Mt Shōwashinzan, the degassing temperature was high so that most of the sulphur was present as sulphur dioxide. On the other hand the equilibrium between hydrogen sulphide and sulphur dioxide may have been established at a low temperature, so that the amount of exhalated sulphur dioxide was much smaller than that of hydrogen sulphide. In the latter case most of the sulphate would be due to oxidation of hydrogen sulphide, and would also have the isotopic ratio of meteoric sulphur.

It may be that the sulphate in volcanic areas such as in the crater lake "Yugama" of Mt Shirane, referred to by Sakai, comes from the oxidation of sulphur dioxide, and hence has a low $^{32}S/^{34}S$ ratio. Previous work on isotope ratios in bore discharges (Rafter, *et al.*, 1958) has also shown that the sulphate in equilibrium with hydrogen sulphide in underground chloride water at Wairakei, has a low $^{32}S/^{34}S$ ratio. On the other hand, one of the authors (T. A. R., unpublished work) has found a high ratio in much of the sulphate at White Island. It is possible that Sakai greatly overestimates the proportion of sulphur exhalated as sulphur dioxide. According to Ellis (1957), the proportion of sulphur dioxide is negligible below 700° C for equilibrium in the typical gas composition that he assumes, and the proportion of sulphur dioxide to hydrogen sulphide is 1:1·5 at 1,200° C and 1 atmosphere, and 1:8 at 1,200° C and 1,000 atmospheres. It seems probable that most of the sulphur continuously supplied to the ocean is due to the oxidation of hydrogen sulphide, and sulphides, of high $^{32}S/^{34}S$ ratio, and not from sulphur dioxide only. The isotopic ratio of the continuously supplied sulphur may thus be nearly equal to that of meteoritic sulphur, which suggests that the isotopic ratio in the sulphate ions of the present ocean has been brought about through some other process such as bacterial activity.

The evidence presented in this paper shows that the exhalations from the volcano, White Island, have an average sulphur isotopic ratio close to that of igneous rocks, so that the contribution of its sulphur to the ocean tends to enrich the ocean in the lighter sulphur isotope with respect to present ocean sulphate. Such additions would support Thode's bacteriological activity theory as a mechanism by which the present ocean has become enriched in the heavier sulphur isotope.

If the bulk of the sulphur that has entered the oceans over geological

time had initially the isotopic ratio of the igneous rocks, 22·15, and by subsequent bacterial activity the present isotopic ratio of ocean water has been established, it can be calculated, assuming a $^{32}S/^{34}S$ ratio of 22·33 as reported for Gulf of Mexico sulphur, that, for a sulphur isotopic balance, an amount of sulphur approximately twice as great as exists as sulphate in the ocean, 10^9 million tons, must exist in the sedimentary deposits.

Conclusions

(1) A method has been developed for satisfactorily sampling fumarole discharge.

(2) In addition to sulphur and sulphate in the discharge, polythionates and sulphite have been identified. These sulphur compounds account for the greater part of the soluble-sulphur in the discharge.

(3) The $\delta^{34}S$ enrichment in the sulphur precipitating out chemically after collection of the discharge, and that collected from around the vent, are isotopically the same. This sulphur is enriched in the lighter isotope of sulphur ^{32}S with respect to the overall average. This evidence suggests that so-called volcanic sulphur is enriched in ^{32}S by chemical reactions at the vent mouth.

(4) Only a small amount of sulphate exists initially in fumarole discharge. This could be accounted for by the combustion of sulphur that always results in a small percentage of SO_3. Variable amounts of sulphate are formed by various oxidation-reduction processes, on cooling, or after collection of the discharge. No significance can be attached to sulphate isotopic ratios in fumarole discharges.

(5) The overall average $^{32}S/^{34}S$ ratio for the sulphur isotopes in six fumaroles has been calculated from quantitative chemical and isotopic data. The average $^{32}S/^{34}S$ value of 22·15 suggests that the parent sulphur material is of igenous origin.

(6) If sulphur from volcanic exhalations can be shown generally to have an average sulphur isotopic ratio similar to that of sulphur in igneous rocks, then these additions of sulphur to the ocean cannot account for the present enrichment of the heavy isotope of sulphur in ocean sulphate.

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AN ATTEMPT TO EXTEND THE OPERATING TEMPERATURE OF COPPER CATHODE GEIGER TUBES

By R. E. BELIN* and A. E. BAINBRIDGE†, Dominion Physical Laboratory, Department of Scientific and Industrial Research, Lower Hutt.

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Summary

The characteristics in the temperature range 20° to 230° C of geiger tubes with oxide-coated cathodes are compared with those whose cathodes have been cleaned by reduction in hydrogen. The outstanding difference between these geiger tubes with initial heating was the absence in the hydrogen-cleaned tube of any increase in pulse rate above normal rate despite a permanently increased threshold voltage. Above 150° C the characteristics of the oxide-coated geiger tubes began to deteriorate, although the hydrogen-reduced tubes could be raised to 230° C without any change in the background rate. At and above 230° C both types of tubes went into a continuous discharge. Suggestions are put forward for a possible mechanism that could cause oxide-coated geiger tubes to deteriorate at a much lower temperature.

INTRODUCTION

A programme of radioactivity well-logging of geothermal bores and a radioactivity survey of hot pools in New Zealand, initiated an investigation of geiger tube characteristics at temperatures up to 260° C.

At the start of the investigation, in 1950, little had been published concerning the effects of temperature on geiger tubes, but much has appeared recently with upper temperature limits ranging from 100° C to 220° C. Fujiako, *et al.* (1950) evacuated copper cathode tubes at 400° C, heated them in an induction furnace to 800° C then filled them with 9cm of Hg of argon and 1cm Hg of alcohol and then reheated them to 220° C. With this method of preparation no initial increase in count rate was observed up to 220° C, but above this temperature the tube went into a continuous discharge. This observation and a general survey of the reports of other workers (Loosemore and Taylor, 1950; Korff, *et al.*, 1942; Parkash and Kapur, 1950; Louw and Maude, 1949; Hereford, 1950; Joshi, 1953; Kimura, 1950 a, b; Meunier, *et al.*, 1955; Blanc and Viste, 1955; Puri and Gill, 1956) suggested that the safe upper limit of operation for an alcohol argon and halogen-noble gas geiger tube (Clark, 1955) would be approximately 200° C.

It was thus apparent that, for operation at higher temperatures

*Now with Snowy Mountain Authority, Australia.
†Now with Division of Nuclear Sciences, D.S.I.R.

(260° C) it would be necessary to extend the upper temperature limit of the geiger tube, or else change the nature of the radiation detector to a proportional counter which has recently been reported (Mojk, *et al.*, 1955) to operate satisfactorily up to 900° C. Proportional counters require high gain amplifiers which must also operate at the high temperatures existing in the geothermal bores. The pulse from a geiger tube requires no amplification, so that this type of detector is preferred. A preliminary investigation into the effect of temperature on geiger tubes was therefore undertaken, and is described below.

EXPERIMENTAL DETAILS

Geiger Tube Classification

Type A. These were of all metal construction, having a copper cathode 18 in. long and 1 in. diameter.

Type B. These had a copper cathode 12 in. long contained in a glass envelope.

Type C. These were identical in construction to type B, except that all the copper oxide had been removed as described in the section on cleaning.

In each type the anodes consisted of 0·006 in. diameter tungsten wire.

Cleaning

The parts of type A were sand-blasted before leaving the workshops and then, prior to assembly, rinsed with water and then alcohol. Types B and C were cleaned internally with a solution of chromic and sulphuric acids and then rinsed in distilled water and alcohol. In addition, the type C tubes were heated to 400° C in a hydrogen atmosphere to remove the copper oxide from the surface, and care taken to exclude any air before filling.

Filling

The tubes were evacuated through a liquid oxygen trap to a pressure of 10^{-3}mm Hg and left pumping for some time to remove as much of the water vapour as possible. After flushing with argon and repumping they were filled with alcohol and argon to partial pressures of 1cm and 9cm Hg respectively.

Measurement of the Threshold Voltage, Pulse Rate, and Plateau

The threshold voltages of the tubes were monitored by measuring the voltage required to maintain the geiger pulses at a constant amplitude (Fergusson, 1953). This voltage, the pulse rate (using a circuit with a paralysis time of 5 millisecs, and the temperature were continuously recorded on a pen recorder. In addition, the pulse rate was checked regularly by means of a scaler. An oscilloscope, with a suitable linear amplifier, was used for visual examination of the tubes. At

desired stages of the experiments, the plateaux of the tubes were measured with an automatic plateau plotter.

Methods of Heating

Two methods of heating the geiger tubes were adopted—an oil bath, and an air oven—depending upon whether it was desired to apply a rapid or a slow temperature increase to the geiger tube. Both the bath and the oven were thermostatically controlled within the temperature range of 20° to 300° C.

Type B tubes could be operated while their anodes were being heated electrically.

RESULTS

Geiger Tubes with Oxide-Coated Cathodes

(1) On heating the tube for the first time the pulse rate increased above normal background. (Normal background is defined as the pulse rate of the geiger tube at room temperature in the absence of any radioactive sources.)

(2) A rapid elevation for a range of temperature up to 150° C of Type A increased the pulse rate by N_0 above normal background. N_0 was proportional to the temperature rise. With type B there was about a one-minute lag between the time of immersion of the tube in the bath and the increase in pulse rate. This lag was assumed to be due to the poor thermal conductivity of the glass.

(3) After immersing the tube in a bath held at any constant temperature up to 150° C the pulse rate gradually returned to normal according to the relation $N_1 t^a = N_0$, where N_1 is the pulse rate, corrected for normal background, at time t. The index a was found to depend on the tube and was approximately equal to 0·8 if t is in minutes. After the pulse rate had returned to normal the tube was considered to be "seasoned".

(4) After the tube had been seasoned at a definite temperature T, ($T < 150°$ C), it could be cycled between room temperature and T without any change in the normal background pulse rate (within the statistics of the experiment) or the life of the tube.

(5) A further increase of temperature above T produced an increase in pulse rate as described in (2) and (3) above.

(6) When the tube was first raised to a constant temperature the threshold voltage rose, rapidly at first and then more slowly, reaching a constant value when the pulse rate had returned to normal background The change of theshold with time for one particular tube is shown in Fig! 1. The relationship between threshold voltage V and time can be represented by $dV/dt = k/t^b$, where b is constant and is approximately equal to unity. The pulse rate N_1 is greatest when dV/dt is greatest, and returns to normal when it is zero. The threshold voltage increase for a temperature rise from 20° to 100° C was different for each tube

examined and was normally in the range of 10 to 50 volts for a tube with an initial threshold voltage of 1,000 volts. When the temperature, after seasoning of the tube, was reduced to room temperature, the threshold voltage never returned to its pre-seasoning value but dropped only a few volts, as indicated in Fig. 1.

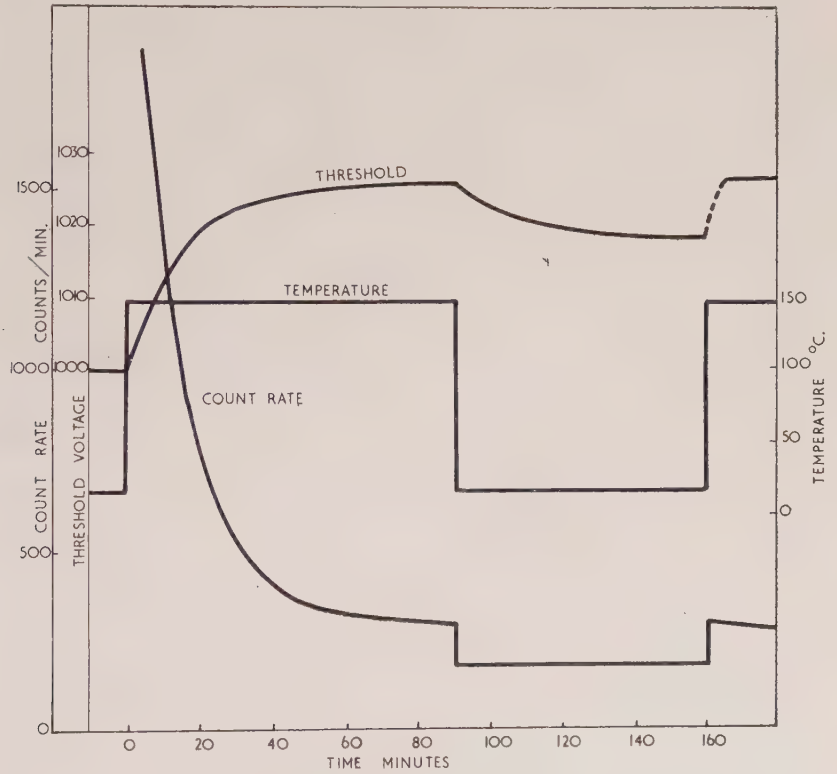

FIG. 1.—Relation of count rate and threshold voltage of a copper oxide coated cathode, with initial temperature change.

(7) If the tube was now cycled between room temperature and 100° C, there was only a 5-volt change in the threshold voltage. The change was proportional to the temperature rise and obeyed the same equation, described in (6) above.

(8) For a seasoned tube, the plateau lengthened and the slope decreased with temperatures up to 150° C.

(9) At temperatures greater than 150° C the background pulse rate behaved in the same manner as explained previously, except that it never quite returned to normal again, but assumed a new higher value which was proportional to the temperature increment above 150° C.

(10) At 230° C the geiger tubes went into continuous discharge and if held in this state for several hours, upon returning to room temperature their plateau slopes increased.

(11) The temperature of the anode of tube Type B could be raised above red heat before any spurious pulses were detected.

Effects (1) to (11) were also observed with tubes constructed with a stainless steel cathode.

Geiger Tubes with Hydrogen-Cleaned Cathodes

For tubes with hydrogen-cleaned cathodes, effects (1) to (6), namely the increase in pulse rate and threshold voltage upon first raising the temperature of the geiger tube up to approximately 230° C, were absent. At 230° C these tubes behaved in the same manner as did those with oxide-coated cathodes (effect 10). Their background pulse rate did not change between 150° C and 230° C.

Small changes in threshold voltages, effect (7) were also observed when temperature cycling a tube with hydrogen-cleaned cathode. The anode temperature could also be raised above red heat, effect (11), before spurious pulses appeared.

Discussion

The increase in pulse rate, effects (1) and (2), the small increase in threshold voltage, effect (7), the plateau improvement, effect (8), and the breakdown above 220° C, have already been reported (Fujioka, *et al.*, 1950).

The decrease in pulse rate of a geiger tube which had a high pulse rate as a result of a temperature increase, effect (3), has been reported to decrease exponentially with the square of time (Kimura, 1950b). No mention has been made that this occurs only once in the history of the tube, effect (4). The relation between rate of change of threshold and pulse rate, effect (6), upon first heating the tube has not been previously reported.

Heating of the anode, effect (11), indicates that the observed phenomena originate at the cathode and not at the anode or in the gas. The small changes in threshold with temperature cycling after the tube has been seasoned, effect (7), support the suggestion of Puri and Gill (1956) that adsorption and desorption of the tube gases is taking place at the cathode surface.

Since geiger tubes with no semi-conductor oxide coating on the cathode surface (Type C) do not exhibit the increase of pulse rate with initial heating, it is probable that the oxide film is an important contributing factor to the phenomena. Brattain and Bardeen (1953) in an investigation of the surface properties of germanium, reported that the work function of a semi-conductor is very dependent on the ambient state (gas, pressure, and temperature) of the surface. They have also reported that electrons can become trapped on germanium con-

taining minute traces of impurities and that they subsequently escape, with a rate that is exponential with time. Kramer (1952) has shown that electrons, as a result of friction or electrical discharge, can become trapped on semi-conductor surfaces and that they can subsequently escape according to the relationship given under effect (3). Fergusson (1953) has also observed that the decay of pulse rate with time after a counter has been subjected to friction follows the same law. These factors associated with the semi-conducting copper oxide film could give a possible explanation of the decay of count rate and the change of threshold with time.

The permanent change of threshold on initial heating, effect (6), is difficult to explain on the basis of adsorption and description because of the rather large increase of pressure, caused by an increased number of molecules in the counter normally required to produce the voltage change. If this were the case the number of molecular layers of alcohol that would be required to be desorbed, assuming a smooth cathode surface, would be of the order of 60 for a 5-volt increase in threshold voltage. A more likely explanation would be the outgassing of water and other gases from the metal cathode and glass envelope. Water would have the most pronounced effect on raising the threshold voltage and within limits will not seriously effect the operation of the geiger tube. Fujioka, *et al.* (1950) as a result of outgassing the glass and metal parts at 400° C and 800° C respectively, did not observe any marked change in threshold voltage or any increase in puse rate when first heating the geiger tube. It is likely that the heating of the authors' tube to 400° C could have produced the same effect in absence of hydrogen cleaning.

CONCLUSION

(1) A comparison has been made between geiger tubes with oxide-coated cathodes with and without treatment at 400° C in a hydrogen atmosphere. It was found that only the treated tubes could be raised to a temperature of 230° C and still give satisfactory operation.

(2) A pulse rate variation has been observed with the oxide-coated tubes. These variations have characteristics that are not unlike those for certain semi-conductors. Since copper oxide is a semi-conductor an investigation of electron emission from the surface may be important in determining the cause of the pulse rate variation and of the upper limit of operation of this type of tube.

(3) A permanent increase in the threshold voltage has been recorded but a satisfactory explanation for this effect cannot be put forward.

(4) A small reversible change in threshold voltage is also observed when the tube undergoes a temperature cycle and this could be satisfactorily explained by the rates of adsorption and desorption of the counter gases on the cathode and glass surfaces, but should be further investigated.

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COCCIDS ASSOCIATED WITH RATA AND KAMAHI IN NEW ZEALAND

By J. M. Hoy, Entomology Division, Department of Scientific and Industrial Research, Palmerston North.

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Summary

A survey was undertaken in an attempt to elucidate the role of coccids in rata and kamahi mortality in the protection forests of Westland and the submontane forests of the southern portion of the North Island. Rata and kamahi were examined throughout their distributional range in the three main islands.

Eight species of coccids, including four apparently new species, are recorded from rata and pohutukawa. Seven species are confined to the genus *Metrosideros* and the remaining species occurs in common both on rata and kamahi. Coccids are considered not to be primary factors in large-scale rata mortality, although *Anoplaspis metrosideri* (Mask.) and *Capulinia orbiculata* n.sp. appear to be seriously deterimental to individual trees when the insects attain high population levels.

Kamahi does not support as many host-specific coccids as does rata. Nine coccid species, including five apparently new forms, are recorded from kamahi. All but three species have been collected on other host plants. The occurrences of the majority of the coccids taken on kamahi are essentially localized. Coccids are not an important factor in kamahi mortality.

Species described in this paper as new to science are *Capulinia orbiculata, Eriococcus rata, E. pohutukawa,* and *E. kamahi.* The remainder of the apparently new species belong to the genera *Coelostomidia, Ctenochiton,* and *Leucaspis.* All these genera require extensive taxonomic revision.

Introduction

For some years a high rate of mortality has been noted in the southern rata (*Metrosideros umbellata* Cav.) and kamahi (*Weinmannia racemosa* Linn.) protection forests in Westland. Similar mortality has been recorded in northern rata (*Metrosideros robusta* A. Cunn.) and kamahi in the submontane forests of the southern portion of the North Island. This mortality has been variously attributed to the ravages of possums, deer, and goats, and to the presence of a scale insect *Anoplaspis metrosideri* (Mask.). To determine the extent of the mortality and to examine contributing factors, an interdepartmental survey of the Westland area was undertaken during February and March 1955. Representatives of the New Zealand Forest Service, the Wildlife Section of the Department of Internal Affairs, and the Soil Bureau, Animal Ecology Section, and Entomology Division of the Department of Scientific and Industrial Research participated. Subsequent to this survey, the writer undertook an examination of the insect complex, particularly coccids (Homoptera: Coccoidea) associated with these tree species throughout the southern portion of the North Island, the South Island, and

Stewart Island. This paper records the coccids associated with rata and kamahi throughout these areas.

Forest Associations

In the North Island submontane forests kamahi is often dominant. Rimu (*Dacrydium cupressinum* Soland.) is present as are other podocarp species. Tawa (*Beilschmiedia tawa* Benth. & Hook, f.) is often an important species at the lower levels, but the forest is characterized by the presence of the northern rata, a large tree of variable habit. Lianes such as *Freycinetia banksii* A. Cunn. and *Metrosideros scandens* Soland. are plentiful as are the ferns. This type of association occurs on Mt. Egmont, the Tararua Range, and in the southern Ruahine Range, apart from the notable absence of *M. scandens* from the last-named locality. Rata and kamahi are also important constitutents of the forests of the central plateau of the North Island. In general, the slopes are not steep and the annual rainfall is between 110 inches and 150 inches.

In the South Island, on the western slopes of the Southern Alps from the Taramakau River south to the Paringa River at altitudes above approximately 800 ft, the southern rata becomes dominant and the numbers of lowland podocarps decrease. Kamahi is plentiful, in some areas a co-dominant, in others, the dominant species. *Carpodetus serratus* Forst., *Coriaria arborea* Lindsay, *Melicytus ramiflorus* Forst. (whitey-wood), *Quintinia acutifolia* T. Kirk, *Fuchsia excorticata* Linn. f., *Nothopanax colensoi* Seem., *Hedycarya arborea* Forst. (pigeon-wood) and *Coprosma* species are prominant in the understory. Tree ferns, blechnums, and supplejack are abundant. A notable feature of this association is the absence of beech. This factor is important, since no trees of a stature comparable to rata and kamahi exist to assume dominance in the event of death of these species.

This association occurs on steep slopes between the altitudes of 800 and 2,500 ft. The slope angle is commonly 45° and in some instances up to 60°. In general, the soils are skeletal, the parent rock being close to the surface. Annual rainfall approaches 200 inches. This protection forest is vital to the economy of Westland, since it serves an important function in moisture conservation, controlling runoff, preventing erosion and consequent aggradation in the rivers.

Southern rata-kamahi forest also occurs in the north-western portion of the South Island, and in eastern and western Southland. In the latter localities the forest is often coastal or semi-coastal as well as montane.

Sites Examined

The original intention was to confine investigation of the insects affecting rata and kamahi to those situations where considerable damage to these tree species had occurred. It was soon apparent that the

FIG. 1.—Map showing localities visited and areas from which specimens were obtained.

insect complex had to be examined over a wider area, particular attention being given to those areas where no visible damage to rata and kamahi had been noted. The localities visited are shown on the

accompanying map (Fig. 1). In addition, officers of the Forest Service submitted samples of rata foliage and stems from the Rowallan, Alton Valley, and Longwoods forests in Southland. Through the courtesy of Mr E. Cutler of the Soil Bureau, D.S.I.R., samples of rata and kamahi foliage and branches were obtained from three localities on Stewart Island.

Throughout the surveyed area in Westland, in protection forest, mortality in rata and kamahi is heavy, particularly in the Kohatahi Gorge (Fig. 2), on the Wilberg Range, Cook Saddle, and Fox

Fig. 2.—Dead rata and kamahi on southerly face of Kokatahi Gorge. In these photographs dead trees show grey.

Glacier areas (Fig. 3). In these regions, a considerable proportion of the rata is dead and perhaps a higher proportion of the kamahi. The majority of the surviving rata appears healthy. This is evident in the commonly occurring almost pure stands of younger, even-age rata seen towards the tops of a number of slopes. Surviving kamahi often showed tip defoliation and a generally unhealthy appearance.

In the majority of areas where death of rata and kamahi is occurring, there has been a general thinning of the canopy, a marked reduction in understory species, apparently due to animals, with a consequent increase in hard fern. Where slipping has occurred, whitey-wood and pigeon-wood appear to be increasing in numbers. In most localities there has been a considerable loss of surface litter, but whether this is due to reduction in numbers of individuals of canopy species, to the

FIG. 3.—Dead rata and kamahi on northerly face above terminus of Fox Glacier.

FIG. 4.—Dead trees on northerly faces above junction of Pohangina River and Piripiri Stream, western Ruahines.

action of animals, or to increased sheet erosion is uncertain. Tree mortality is light in the Franz Josef region, where pressure from animals is markedly less than in other localities.

In eastern and western Southland areas, no marked damage to rata and kamahi was observed and the situation on Stewart Island is reported to be the same.

In the North Island forests, severe damage occurs on both the eastern and western (Fig. 4) faces of the southern Ruahine Range. In the other forests examined, mortality levels are lower, but in these areas it is difficult to assess damage since the presence of a greater variety of other large tree species tends to mask the situation in relation to rata and kamahi. A notable feature, especially in the southern Ruahine Range, is the unhealthy condition of the surviving rata, most living ratas in this area showing considerable branch die-back, particularly on the lower portions of the tree.

FACTORS INFLUENCING THE SITUATION

While a detailed discussion of factors other than insects is outside the scope of this paper, brief reference must be made to those that appear important. It has been suggested that the ratas in severely affected localities are overmature. On steeper slopes the larger trees appear more susceptible than the younger ones. In some areas, notably the Wilberg Range, Cook Saddle, and Fox Glacier, there are almost pure stands of young rata on steep slopes which appear quite healthy. On the flatter ridge tops on the Wilberg Range there are numerous large ratas which are unaffected. In the North Island, mortality is occurring in ratas of all sizes and presumably of all ages. Both in Westland and North Island regions kamahi in all stages other than juvenile, is apparently affected in equal proportions.

Tree mortality in both species in Westland is highest on steep slopes between 40° and 60°. It is possible that with increasing size trees tend to lose their root hold and to lean out from the slope. The skeletal nature of most of the soils would aggravate this condition. In North Island areas, mortality does not appear to be related to slope, as many trees being dead on flat areas as on slopes.

In the Wilberg and Fox areas tree mortality is highest on slopes with a northerly aspect. In the Kokatahi Gorge severe mortality is occurring on slopes with southerly as well as northerly aspect. In the North Island slope aspect does not appear to affect mortality levels.

The presence of animals has markedly upset the equilibrium of the protection forests in Westland. Deer and goats were present in the northern valleys examined, goats alone between Ross and Whataroa and deer in the south. Possums were present in all localities in Westland and in the North Island forests. In general, where severe mortality is occuring in rata and kamahi the level of possum feeding appears to be high.

INSECTS

The major difficulty encountered in adequately sampling the insect population has been the collection of suitable specimens of canopy foliage, particularly from rata. The southern rata cannot usually be climbed and, after much trial and error, samples were obtained by

shooting down branches with a rifle. In this way branches up to 1 inch in diameter were collected, although the fibrous nature of the rata wood made final separation from the tree difficult. In only a few cases were true canopy samples obtained from southern rata. The northern rata has a different growth form which enables a small proportion of trees to be climbed to a height of 50 to 60 ft. Even at this height samples could be taken only from lower branches.

Where the vertical distribution of insects is uneven, as it must be in most instances, or where the insect population is low, inadequate material may be responsible for the apparent absence or infrequent occurrence of certain species in some localities.

A puzzling feature of the insect situation in Westland is the disparity between evidence of the presence of coccids on trees and the numbers collected. This was most noticeable in the Fox Glacier region, where rata mortality is heavy. Many branches heavily coated with sooty moulds were observed and, although samples were taken, no coccids were recovered from rata in that area.

COCCIDS ASSOCIATED WITH *Metrosideros*

A number of coccid species have been reported as attacking members of the genus *Metrosideros*. The most comprehensive list is that of Green (1918) in which he lists *Eriococcus pallidus* Mask., *Coccus hesperidum* (Linn.), *Lecanochiton metrosideri* Mask., *L. minor* Mask., *Chrysomphalus dictyospermi* Morg. and *Anoplaspis metrosideri* (Mask.). To this list must be added *Anoplaspis maskelli* Morris., this species being separated (Morris., 1922) from Maskell's material of *A. metrosideri*. *Coccus hesperidum* and *Chrysomphalus dictyospermi* are cosmopolitan species and, since Green does not list his source of information, it is not possible to ascertain whether these species were recorded on *Metrosideros* in New Zealand or overseas.

Anoplaspis metrosideri (Mask.)

Anoplaspis metrosideri is always located on the leaf (Fig. 5), more commonly on the upper surface. The test is white, waxen, shining, and pyriform with the first and second nymphal exuviae attached at one end. The male test is nearly parallel sided, much smaller, occurring either near the leaf edge or in clusters on the under surface. The adult female is dark brown to black in colour. Nymphs are commonly found attached to the leaf beneath tests of dead females. The male is dark purple with prominent ocelli and a long conspicuous abdominal spike.

This scale has been considered in the past to be directly responsible for death in rata in Westland. Miller (1925) reported heavy infestations of *A. metrosideri* near Lake Kanieri on the slopes of Mt. Tuhua, the trees being either dead or dying. Similar verbal statements have been made about the degree of infestation in this area in recent years, particularly on trees on the northern aspect of the Kokatahi Gorge.

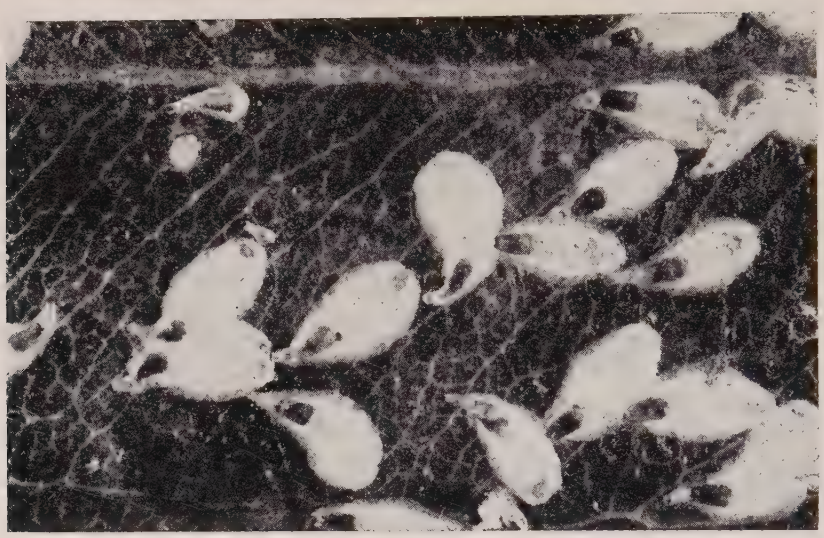

FIG. 5.—*Anoplaspis metrosideri* on leaf of *Metrosideros robusta*.

At the time of the survey almost all these trees were dead. It seems probable that when high populations of *A. metrosideri* are present the insect has a harmful effect on ratas.

During the survey no heavy infestations of this scale were noted, apart from occasional individual trees. There did not appear to be any marked variations in the population levels of *A. metrosideri* between areas in which rata mortality was high and areas where the trees were not dying.

Although no parasites were found in collected material, holes in the tests of many specimens, particularly those from the Franz Josef area, indicate that the species is parasitized.

LOCALITY RECORDS—*Anoplaspis metrosideri*

HOST PLANT—*Metrosideros robusta*

Wellington, 1879, W. Maskell; Motueka, 8/2/20, G. Brittin; Wellington, 18/5/21, J. G. Myers (Green, 1928); Pohangina Valley, 7/4/55*; Mt Egmont, 14/4/55; Colville, 6/8/57.

HOST PLANT—*Metrosideros umbellata*

Wilberg Range, 21/2/55; Franz Josef, 1/3/55; Cook Saddle, 1/3/55; Kokatahi Gorge, 2/3/55; Waimea Forest, 3/3/55; Maclennan, 6/10/55; Chaslands, 6/10/55; Tautuku Bay, 6/10/55;

*In locality records where no mention is made of the collector, specimens were taken by the writer.

Alton Valley, 10/10/55, Forest Service; Rowallan Forest, 10/10/55, F.S.; Lonneker Bay, Nov. 1955, E. Cutler; Kaipipi, Nov. 1955, E. Cutler; 5 miles west of Oban, Nov. 1955, E. Cutler.

Anoplaspis maskelli Morrison

Morrison (1922) described this species from Maskell's material which was labelled as collected from *Metrosideros*. *A. maskelli* was not taken during the current survey. Brittin states in unpublished notes now held by Entomology Division, D.S.I.R., that this species is found only on *M. scandens* and records its occurrence at Ohakune, Wellington, and Motueka. Apparently *A. metrosideri* does not occur on *M. scandens*.

LOCALITY RECORD—*Anoplaspis maskelli*

HOST PLANT—*Metrosideros scandens*
Moteuka, no date, G. Brittin (Green, 1929).

Lecanochiton metrosideri Maskell

This species apparently retains the second nymphal exuviae which becomes incorporated in the dorsum of the female, the dorsum is strongly chitinised and a test in the true sense is apparently absent. First instar nymphs are yellowish, transparent; the second instar and adult females are dark brown in colour. Where the population levels of *A. metrosideri* are high, *L. metrosideri* is more frequently found on the smaller stems. Where the population levels of both species are lower *L. metrosideri* is usually found on the leaf. This insect is subcircular in outline and strongly convex on the dorsum.

Males construct glassy tests on the leaves and stems. The appearance of second instar male nymphs is so radically different from the female that they could easily be taken for different species. Male nymphs are heavily parasitised.

Although *L. metrosideri* is widely distributed the population levels at the time of the survey were very low. It is doubtful whether this species is particularly harmful to rata.

LOCALITY RECORDS—*Lecanochiton metrosideri*

HOST PLANT—*Metrosideros robusta*
Pohangina Valley, 7/4/55; Colville, 6/8/57.

HOST PLANT—*Metrosideros umbellata*
Wilberg Range, 21/2/55; Franz Josef, 1/3/55; Cook Saddle, 1/3/55; Kokatahi Gorge, 2/3/55; Waimea Forest, 3//3/55; Tautuku Bay, 6/10/55; Alton Valley, 10//10/55, F.S.; Devil's Staircase, Lake Wakatipu, 10/10/55; Otira, 28/12/15, G. Brittin.

HOST PLANT—*Metrosideros excelsa*
Auckland, 1882, W. Maskell; Kawau Island, 25/8/55, R. A. Harrison.

HOST PLANT—*Metrosideros* species undetermined.
Milford Sound, 1881, W. Maskell; Maruia, 28/11/35, G. Brittin.

Lecanochiton minor Maskell

L. minor can readily be separated from the preceding species by its appearance on the host plant, the dorsum of the female is flat with an angled edge. The second nymphal exuviae extends almost the full width of the flattened portion of the dorsum. This species occurs in similar situations to *L. metrosideri* on the plant. Mixed populations of *Lecanochiton* species were collected at a number of places. In general, population levels with this species were even lower than those of *L. metrosideri.*

LOCALITY RECORDS—*Lecanochiton minor*

HOST PLANT—*Metrosideros robusta*
Reefton, 1890, W. Maskell; Pohangina Valley, 22/4/55; Colville, 6/8/57.

HOST PLANT—*Metrosideros umbellata*
Wilberg Range, 21/2/55; Franz Josef, 1/3/55; Cook Saddle, 1/3/55; Kokatahi Gorge, 2/3/55.

HOST PLANT—*Metrosideros excelsa*
Amodeo Bay, 6/8/57.

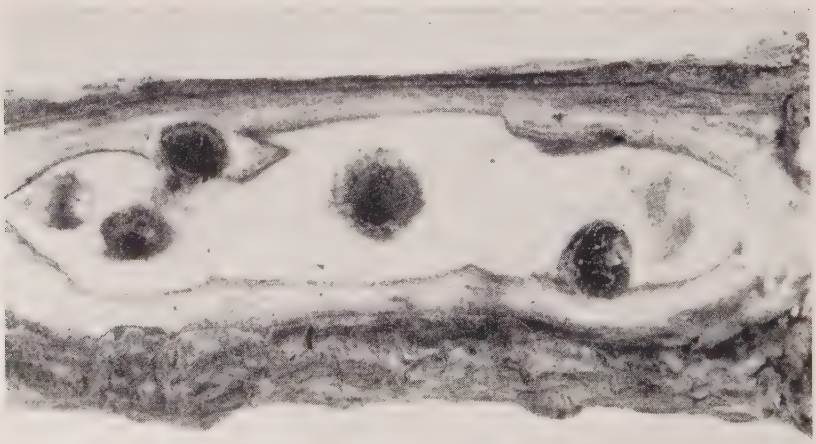

FIG. 6.—Pits in cambium of *Metrosideros robusta* caused by *Capulinia orbiculata* n.sp.

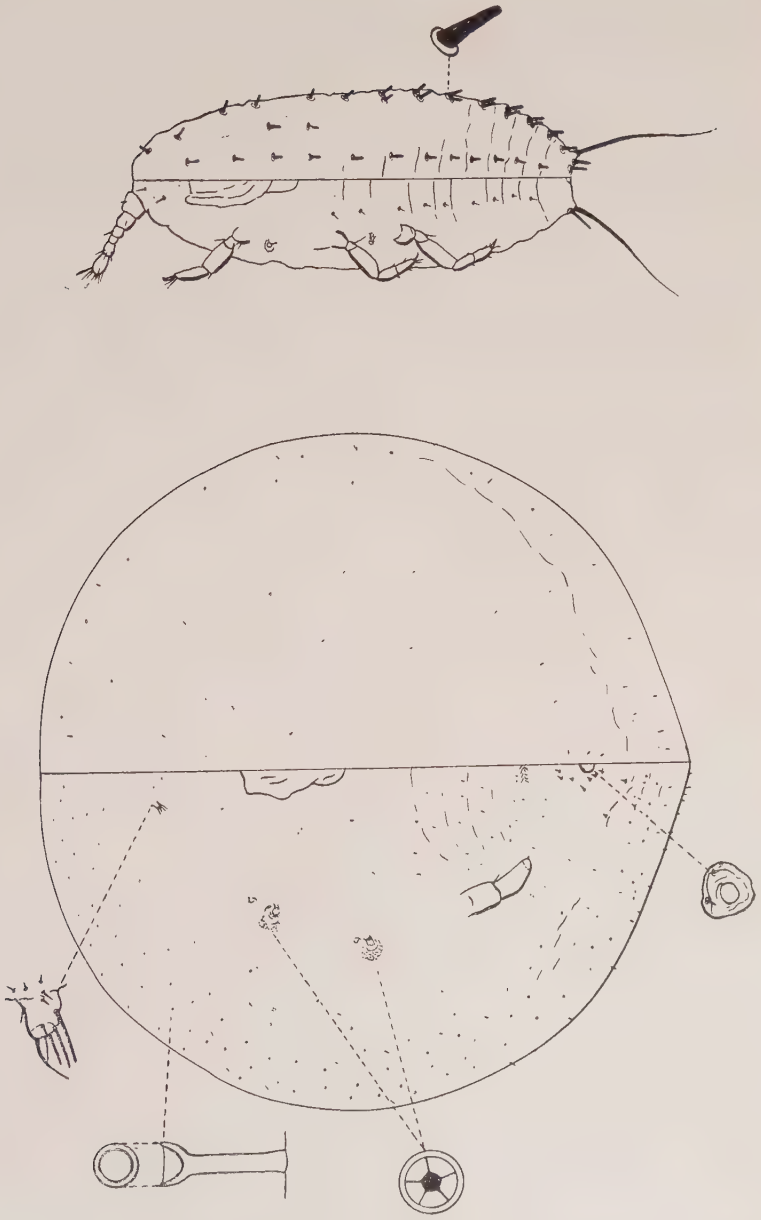

FIG. 7.—*Capulinia orbiculata* n.sp., adult female and first stage nymph (dorsal and ventral view).

Capulinia orbiculata n.sp. (Fig. 7)

This unusual insect is without doubt the most common coccid on both *M. robusta* and *M. umbellata*. There are no external manifestations of its appearance on the tree, it occurs in circular depressions in the bark and cambium (Fig. 6). The adult female (Fig. 7) is circular in outline, and where confined on the host, tends to assume the shape of the cavity occupied. Some powdery wax is found in the depressions occupied by the insect but no test is present. Colour is cream to pale lemon. Length, on slide, ranging from 1·0 to 1·5 mm. The derm is thin and membranous, at maturity there is evidence of strong sclerotisation around the body margin, particularly in the anal region. Extremely fine spicules occur on the dorsal surface.

Only the thoracic spiracles are present, these relatively large and conspicuous, each spiracle is accompanied by a group of quinquelocular pores, the number of pores varying between 22 and 56. The quinquelocular pores have a thickened rim and the pore has appreciable depth, the loculi being set in a shallow cup-shaped depression. Pores of this type occur only in association with the spiracles. The tubular ducts have a simple circular opening to the exterior, the inner extremity is expanded into a cup. No evidence could be seen of a duct from the rim of the cup leading to the gland lumen. Tubular ducts present in moderate numbers on the venter with a concentration towards the lateral margins, relatively few ducts on dorsum.

Setae of both dorsum and venter short and fine, occurring sparsely with some concentration on the venter in the anal area. The anal ring, which is situated on the venter, is simple, consisting of a weakly sclerotised area accompanied by 2 very small setae. The anterior and middle pair of legs are reduced to small inconspicuous tubercules situated anterior to each of the thoracic spiracles, posterior legs in the form of elongate processes still retaining some evidence of segmentation. Antennae reduced to small tubercules with little indication of segmentation, there are 5 terminal setae.

The antennae of the first stage nymph (Fig. 7) are 6-segmented, the legs conform to the usual type. The posterior portion of the lateral margin is beset with a double row of stout blunt setae, the anterior portion with a single row of similar setae. A double row of the same type of setae occurs along the median line of the dorsum. No pores or tubular ducts were detected in the first stage nymph.

The genus *Capulinia* Signoret contains 3 species from the central American region. As far as is known all 3 species occur on Myrtaceae, 2 species, *C. crateraformans* Hemp. and *C. jaboticabae* von Iher. occurring in the same situations on the plant as does the New Zealand species, *C. sallei* Sign., the genotype, occurs on the leaf. Ferris (1955) in listing the recognition characters of the genus notes that the thoracic spiracles are unaccompanied by pores. *C. orbiculata* has a number of quinquelocular pores associated with each of the thoracic spiracles.

Few specimens of *C. orbiculata* have been collected from smaller

stems, infestation appears to be heaviest on branches above $\frac{3}{4}$ inch in diameter, being common on branches up to 3 inches in diameter. This coccid has been found at all localities where branches more than $\frac{3}{4}$ inch were collected. Unfortunately, on account of weight and bulk, few branches of this size were taken during the Westland survey, but *C. orbiculata* was recorded where such branches were collected.

In view of the wide distribution of this insect, both where rata mortality is occurring and in areas where it is not, *C. orbiculata* cannot be implicated as a primary cause of tree mortality.

LOCALITY RECORDS—*Capulinia orbiculata*

HOST PLANT—*Metrosideros robusta*

Pohangina Valley, 7/4/55; Mt. Egmont, 14/4/55; Tamaki Stream, 19/4/55; Manawatu Gorge, 19/4/55; Colville, 6/8/57.

HOST PLANT—*Metrosideros umbellata*

Kokatahi Gorge, 2/3/55; Waimea Forest, 3/3/55; Maclennan, 6/10/55; Chaslands, 6/10/55; Tautuku Bay, 6/10/55; Upper Hollyford Valley, 9/10/55; Alton Valley, 10/10/55, F. S.; Rowallan Forest, 10/10/55, F.S.; Devil's Staircase, 10/10/55; Lonneker Bay, Nov. 1955, E. Cutler; Kaipipi, Nov. 1955, E. Cutler.

TYPE LOCALITY—Pohanagina Valley.

Holotype and paratypes in collection of Entomolgy Division, Palmerston North.

Eriococcus rata n.sp. (Fig. 8)

The ovisac of the female is tough and heavily felted, similar in colour to the bark of the host plant. Adult females are found in the stem and leaf axils and in bark crevices. Length, on slide, about 1·65 mm. Body shape is rotund. The derm of the dorsum has a fish-scaled appearance, particularly on the abdominal region, the anal lobes are well sclerotised. Enlarged setae are confined to the margin of the dorsum. Marginal setae on the abdomen occur, 2 to each segment. The remaining dorsal setae are few in number, small, and slender. Sessile pores on the venter vary in number of loculi between 5 and 9, by far the most common number of loculi being 7; the rim of these pores is not markedly sclerotised. Tubular ducts are very numerous on the dorsum, while small numbers occur on the margins of the venter. The cellular gland structure associated with the ducts shows prominently under phase constrast. The cup of the ducts is noticeably asymmetrical. The antennae are six segmented, the third segment being the longest. The coxa and distal portion of the femur of the posterior legs have a number of pores on the dorsal face. The anal ring has eight setae. The dorsal setae of the anal lobes are slightly longer than the marginal setae. The tarsal claws have a small tooth.

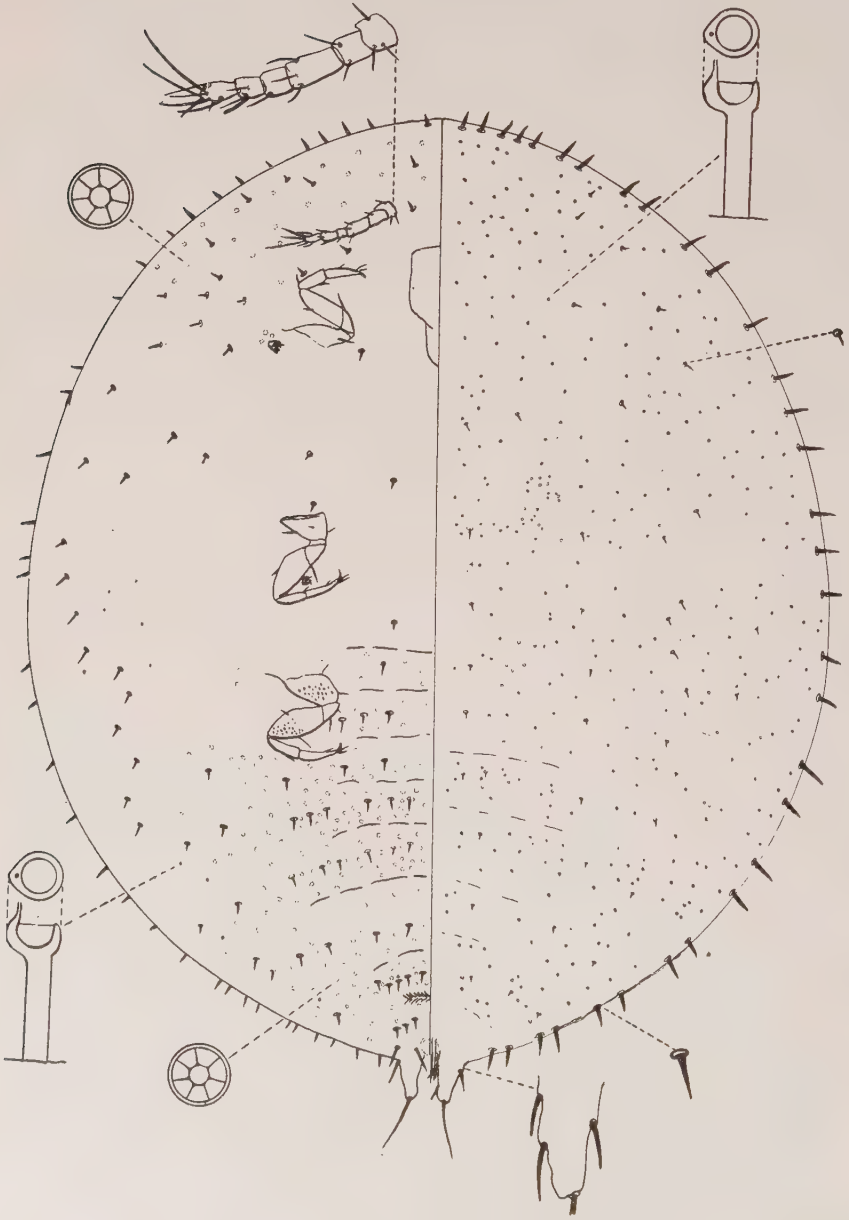

FIG. 8.—*Eriococcus rata* n.sp., adult female (dorsal and ventral view).

Eriococcus rata was not collected in the South Island during this survey but both the Maskell and Brittin collections contain specimens from *Metrosideros*. Slides in the Maskell collection bear the label *E. pallidus var. metrosideri,* the insect bears little similarity to *E. pallidus.*

Locality records—*Eriococcus rata*

Host plant—*Metrosideros robusta*

Pohangina Valley, 7/4/55; Mt. Egmont, 14/4/55; Tamaki Stream, 19/4/55.

Host plant—*Metrosideros* species not stated.

No locality, 1894, W. Maskell; Westport, May 1932 and 11/10/35, G. Brittin.

Type locality—Pohangina Valley.

Holotype and paratypes in collection of Entomology Division, Palmerston North.

Eriococcus pohutukawa n.sp. (Fig. 9)

During the course of this survey, plants of *Metrosideros excelsa* Sol. ex Guertn. (pohutukawa) were examined at a number of places. In almost all cases these plants were infested by a species of *Eriococcus.* The sac of the adult female, which is closely felted, occurs in the leaf axils and in crevices in the bark, occasionally on the leaf surface. Length, on slide, about 1·55 mm. Body shape is elongate oval. The dorsal derm presents a fish-scaled effect similar to that of *E. rata.* Setae of the dorsal marginal fringe are more numerous than in *E. rata.* There is a considerable variation in size in the marginal setae but all are sharp tipped with a slightly expanded base. The dorsal body setae show a variation in size but are much more numerous and prominent than those of *E. rata.* As in *E. rata,* the number of loculi in the ventral pores varies between 5 and 9, by far the most common number being 7. The rim of the pore is sclerotised and quite prominent. Tubular ducts not so numerous as in *E. rata,* the cup is asymmetrical and the tube leading to the gland lumen is long, the cellular structure of the gland shows prominently under phase contrast. The antennae are 6-segmented, the 3rd segment being the longest. The coxa and distal portion of the femur of the posterior legs beset with pores on the dorsal face. Anal ring with 8 setae. Dorsal setae of anal lobes slightly smaller than marginal setae. Tarsal claw with tooth.

This species has been implicated in the death of a number of pohutukawas at New Plymouth.

Locality records—*Eriococcus pohutukawa*

Host plant—*Metrosideros excelsa*

Wāihi, 26/3/34, G. Brittin; Opunake, 14/5/55; New Plymouth, 15/4/55; Kawau Island, 25/8/55, R. A. Harrison; Spirits Bay, 10/1/57; Maunganui Bluff, 22/1/57.

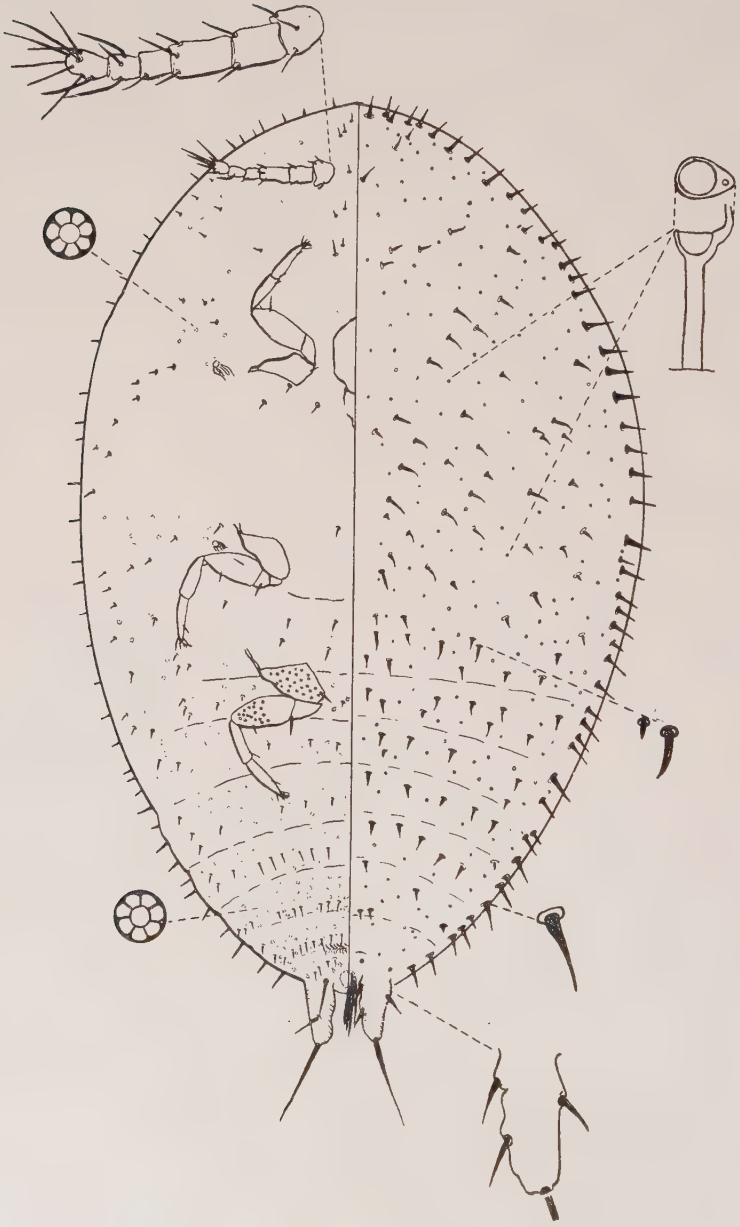

FIG. 9.—*Eriococcus pohutukawa* n.sp., adult female (dorsal and ventral view).

HOST PLANT—not recorded.
Auckland, February 1921, G. Brittin.

TYPE LOCALITY—New Plymouth.
Holotype and paratypes in collection of Entomology Division, Palmerston North.

Coelostomidia species, near ***pilosa*** (Mask.)

A species of *Coelostomidia* was present on southern rata at a number of localities in Westland. The same species also occurs on kamahi. Although population levels were low, this insect was responsible for the production of honeydew supporting most of the sooty mould observed on ratas in these areas.

LOCALITY RECORDS—*Coelostomidia* species

HOST PLANT—*Metrosideros umbellata*
Franz Josef, 1/3/55; Cook Saddle, 1/3/55; Kokatahi Gorge, 2/3/55; Waimea Forest, 3/3/55.

COCCIDS ASSOCIATED WITH *Weinmannia*

There are no published records of coccids attacking either *Weinmannia racemosa* or *W. sylvicola*. During this survey a diverse range of coccids were collected from *W. racemosa*, but with few exceptions the population levels were low and it was unlikely that the scale insects were severely affecting the trees. Most of the coccids species collected from *Weinmannia* were species known to occur on other host plants, or collected from other hosts during this study. It would appear that the genus *Weinmannia* does not support a range of host-specific coccid species in the same fashion as does the genus *Metrosideros*.

Coelostomidia species, near ***pilosa*** (Mask.)

This species is the same as that occurring on southern rata, but on kamahi it occurs more commonly and at higher population levels. It was collected on kamahi stems and in stem galls, apparently the coccid is not responsible for the production of the galls which were sometimes occupied by other insects, notably mycetophagid larvae. As on rata, the honeydew produced by this species supported a heavy growth of *Capnodium* fungi.

LOCALITY RECORDS—*Coelostomidia* species

HOST PLANT—*Weinmannia racemosa*
Wilberg Range, 21/2/55; Fox, 28/2/55; Cook Saddle, 1/3/55; Kokatahi Gorge, 1/3/55; Pohangina Valley, 22/4/55; Ratanui, 6/10/55.

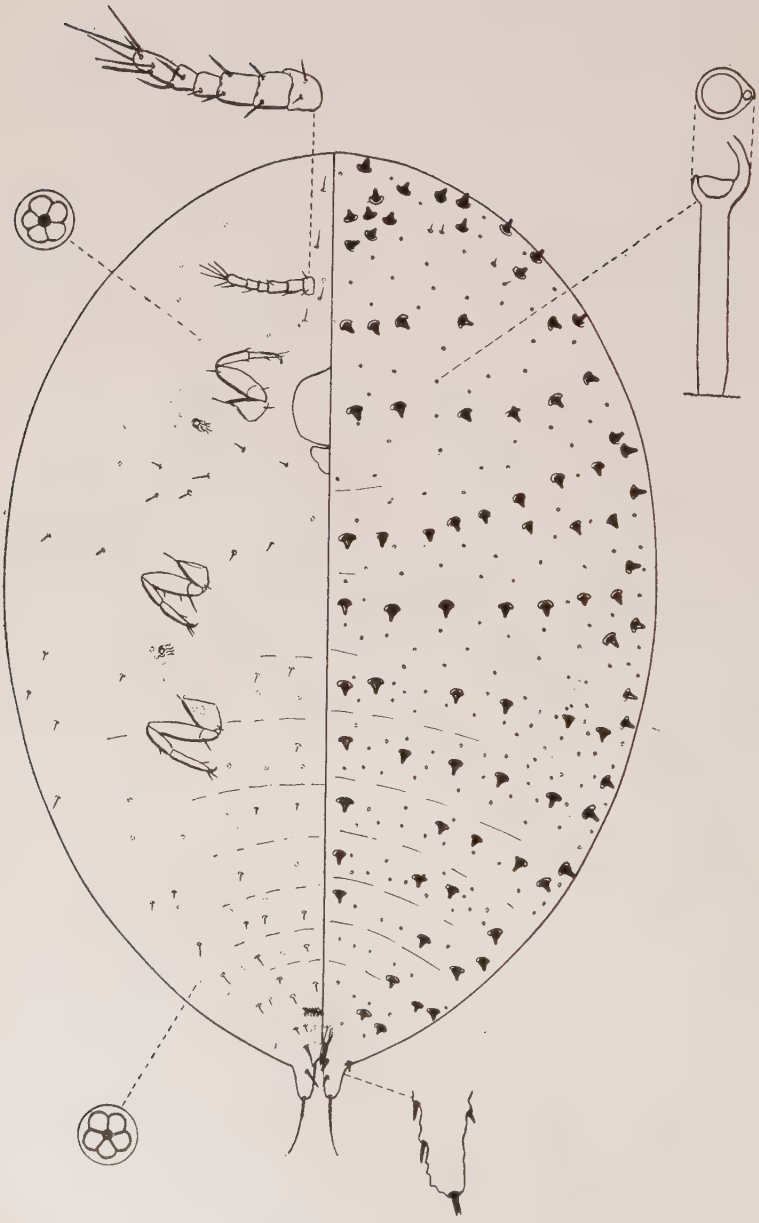

FIG. 10.—*Eriococcus kamahi* n.sp., adult female (dorsal and ventral view).

Eriococcus kamahi n.sp. (Fig. 10)

The sac of the female is grey and felted, occurring in the stem and leaf axils. The adult female is about 1·15 mm. in length, on slide. Dorsum beset with moderate numbers of short, stout, broadly based, blunt-tipped setae, these arranged in tranverse rows except for marginal setae. Quinquelocular pores on the venter, not numerous, each with relatively prominent lightly sclerotised rim. Tubular ducts on dorsum somewhat variable in shape of cup at inner extremity and in the position of the tube leading to the gland lumen. The majority of ducts are similar to that shown in Fig. 10, but some are more markedly asymmetrical, with the tube projecting from the side of the cup. Anal ring with 6 setae, these longer than the anal lobes. Anal lobes are moderately sclerotised, the seta on the outer margin of the dorsal face shorter and more slender than those of the dorsum, setae on the inner margin more slender than those of the dorsum. Apical inner margin of lobes with a toothed appearance. Antennae 6-segmented, the 3rd segment not longer than the apical segment. Coxae of posterior legs with pores. Claw with a small tooth.

Eriococcus kamahi does not appear to build up to high population levels, it cannot be considered an important factor in kamahi mortality.

LOCALITY RECORDS—*Eriococcus kamahi*

HOST PLANT—*Weinmannia racemosa*
Wilberg Range, 21/2/55; Tamaki Stream, 19/4/55; Riverton, 7/10/55; Pohangina Valley, 22/7/57; Waituhi Saddle, 8/8/57.

TYPE LOCALITY—Pohangina Valley.
Holotype and paratypes in collection of Entomology Division, Palmerston North.

Eriochiton hispidus Mask.

E. hispidus was collected from kamahi at 3 localities. The insect occurs on the larger stems, sometimes in bark crevices, sometimes on the surface. The adult female is dark brown in colour, the test is apparently absent, the body being fringed with white wax.

LOCALITY RECORDS—*Eriochiton hispidus*

HOST PLANT—*Weinmannia racemosa*
Pohangina Valley, 25/4/55; Riverton, 7/10/55; Waituhi Saddle, 8/8/57.

Ctenochiton flavus Mask.

This lecanid was present in small numbers at three North Island localities.

LOCALITY RECORDS—*Ctenochiton flavus*

HOST PLANT—*Weinmannia racemosa*
Pohangina Valley, 25/4/55; Tamaki Stream, 19/4/55; Waituhi Saddle, 8/8/57.

Ctenochiton species, near ***flavus*** Mask.

Another *Chenochiton* species occurs sparsely on the leaves of kamahi in one area. This insect can be separated from *C. flavus* by the unusually small number of pores in the spiracular canellae.

LOCALITY RECORD—*Ctenochiton* species

HOST PLANT—*Weinmannia racemosa*
Nukumaru, 15/4/55.

Hemiberlesia rapax (Comstock)

This cosmopolitan species occurs on the smaller stems of kamahi, commonly in the leaf axils, occasionally on the upper leaf surfaces.

LOCALITY RECORDS—*Hemiberlesia rapax*

HOST PLANT—*Weinmannia racemosa*
Nukumaru, 15/4/55; Pohangina Valley, 22/4/55.

Lepidosaphes pyriformis (Mask.)

L. pyriformis has been recorded from a wide range of hosts. During this survey it was taken on kamahi at two localities in the North Island. The scale occurs commonly on the upper leaf surface and on the stem in smaller numbers.

LOCALITY RECORDS—*Lepidosaphes pyriformis*

HOST PLANT—*Weinmannia racemosa*
Nukumaru, 15/4/55; Waituhi Saddle, 8/8/57.

Leucaspis species A, near ***L. maskelli*** Britt.

This insect, which differs from *L. maskelli* in the shape of the pygidium, was taken on kamahi stems at one North Island locality.

LOCALITY RECORD—*Leucaspis* species A

HOST PLANT—*Weinmannia racemosa*
Nukumaru, 15/4/55.

Leucaspis species B

Another *Leucaspis* species belonging to the same general group as *L. maskelli* but differing from any of the described species of the genus was taken at two places. This insect occurs in moderate numbers on the smaller stems of the host plant.

LOCALITY RECORDS—*Leucaspis* species B

HOST PLANT—*Weinmannia racemosa*
Pohangina Valley, 22/4/55; Waituhi Saddle, 8/8/57.

DISCUSSION

Eight species of coccids are recorded from the genus *Metrosideros,* 7 of these species are apparently confined to that genus while 1 species (*Coelostomidia* species) occurs in common both on rata and kamahi. All of the scale insects affecting rata and pohutukawa have a wide distribution, being taken throughout the entire distributional range of the host plants in New Zealand.

Four species are apparently new, 1 of these, *Capulinia orbiculata,* reaches high population densities and causes considerable damage to the cambial layers in rata. *Eriococcus rata* has never been seen at high population levels on rata and is not considered to be a particularly important factor in rata mortality. *Eriococcus pohutukawa* has been implicated in the death of pohutukawas; in this instance it was the only insect present. Affected trees sprayed with white oil recovered, whilst unsprayed trees died. This insect has not been collected from rata. *Coelostomidia* species was not recovered in large numbers from rata; although this insect is responsible for the production of conspicuous sooty mould on the trees, it cannot be regarded as an important factor in tree mortality.

Anoplaspis metrosideri, although widespread, occurred at low population densities except in one or two instances where high populations were found only on small numbers of trees. Where there is a heavy infestation with this insect trees appear unhealthy. From the time of the survey over the subsequent two years there has not been any major change in the population level of *A. metrosideri* on specimen trees under periodic observation. *A. maskelli* is apparently confined to *Metrosideros scandens* and is therefore not a factor in tree rata mortality. There is no indication that either *Lecanochiton metrosideri* or *L. minor* occur in high enough numbers to have an adverse effect on either rata or pohutukawa.

A sufficiently large sample of the principal rata areas of all three main islands has been examined to allow conclusions to be drawn on the role of coccids in rata mortality. Apart from isolated cases of individual trees there appears to be little detectable difference in either the distribution of the principal coccid species or in population levels

between areas in which the rata is healthy and those areas where rata mortality is high. It would appear that coccids are not the primary factor in rata mortality, but it is possible that in some areas these insects play an important secondary role where trees are weakened from some other cause.

Nine coccid species are recorded from the genus *Weinmania*. In all cases where these insects can be given specific identity the coccids are known from a wide range of host plants. Five of the 9 species recorded are apparently new. Of course, *Coelostomidia* species also occurs on rata, *Leucaspis* species B occurs on tawa. *Ctenochiton* species, *Eriococcus kamahi*, and *Leucaspis* species A have not been recorded from plants other than *Weinmannia racemosa*.

In New Zealand the genus *Weinmannia* does not appear to support a specialised coccid fauna of its own, as does the genus *Metrosideros*. It is interesting to note that in most cases the coccids reported from kamahi are essentially local in occurrence, being much more common in forest remnants or in re-growth than in large forest areas. A relatively high proportion of kamahi is dead or dying in the protection forests of Westland and in the submontane forests of the southern portion of the North Island in the absence of any coccid common to all of these areas. This in itself is an indication of the secondary nature, if any, of coccid effect on kamahi.

Ctenochiton species and two species of *Leucaspis* occurring on kamahi as well as the *Coelostomidia* species common to rata and kamahi have not been described as new. The genera containing these insects require taxonomic revision, and descriptions of apparently new species are reserved until such revision can be undertaken.

It is emphasised that this paper deals with only one facet of what appears to be a very complex situation. It is probable that the extensive mortality occurring in rata and kamahi is due to a combination of factors. This survey shows that coccids are apparently not the primary cause.

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THE SPECTROPHOTOMETRIC DETERMINATION OF MOLYBDENUM, TUNGSTEN, AND VANADIUM IN SOILS AND PLANTS

PART I—IN SOILS*

By J. H. Watkinson, Rukuhia Soil Research Station, Department of Agriculture, Hamilton.

(Received for publication, 13 November 1957)

Summary

A spectrophotometric method for determining molybdenum, tungsten, and vanadium in soils from one aliquot of solution is described. Molybdenum and tungsten, complexed with citric acid, are separated from vanadium and most elements that would interfere in their subsequent determination by passing the soil extract through a cation-exchange resin. The molybdenum and tungsten in the effluent are then separated chromatographically on an anion-exchange resin column and determined by the dithiol method. After being eluted from the resin column free of interfering elements, the vanadium is determined by the phosphotungstate method.

Introduction

In the last ten years, responses of pasture to small amounts of each of the elements molybdenum, tungsten, and vanadium have been reported from various parts of New Zealand. The responses to molybdenum have been outstanding. To study the role played by these elements, a reasonably rapid and accurate method for determining them in soils and plants is required. Determining all three from the same solution is not only a means of saving time, but a necessity when the sample is small. Hence the analytical method finally adopted, and now to be discussed, was designed to incorporate this feature.

Amounts Occurring in the Soil

Goldschmidt (1954) gives the average content of the lithosphere for molybdenum, tungsten, and vanadium as being 2·3 p.p.m., 1 p.p.m., and 150 p.p.m. respectively. The normal molybdenum and vanadium contents of soils are given by Swaine (1955) as ranging from 0·2 to 5 p.p.m., and 20 to 500 p.p.m. respectively. He cites no values for tungsten in agricultural soils. The molybdenum content of New Zealand soils covers the range 0·1 to 10 p.p.m. (e.g. Grigg, 1953, Mr N. Wells, pers. comm.), while the vanadium content varies from 1 to

*The substance of a paper presented at the A.N.Z.A.A.S. Conference, 1957.

300 p.p.m. (Mr N. Wells, pers. comm.). Assuming Goldschmidt's ratio, and that tungsten is distributed in a similar fashion to molybdenum, then the tungsten content of soil would be expected to be about half that of molybdenum. Thus, there is the problem of measuring micro-amounts of these elements in the presence of a large amount of a very wide mixture of other elements. For instance, the ratio of iron to molybdenum is invariably much greater than in molybdenum steels. In this paper only spectrophotometric methods of analysis are considered.

Methods Available

There are a number of good methods by which any one of the elements could be determined (Sandell, 1950). In one instance—the dithiol method of Allen and Hamilton (1952) for biological material—both molybdenum and tungsten are determined together. Unfortunately this method is inapplicable to soils because of their much higher iron content. Iron is specially removed in the dithiol method of Williams (1955) for the determination of molybdenum in soils, and this procedure may allow for the determination of tungsten as well. There is, however, no procedure for measuring the three metals, molybdenum, tungsten, and vanadium, together.

In its macro-determination, molybdenum has been quantitatively separated from iron in ores and alloys (e.g. Alimarin and Medvedeva, 1955a and Klement, 1952) and, in pure solutions, from vanadium (Klement, 1952) by means of cation-exchange resins. Also, the interactions of molybdenum and tungsten with cation-exchange resins are very similar (Alimarin and Medvedeva, 1955a, Lur'e and Filippova, 1947, Samuelson, 1953, pp. 136, 141-2). Thus, it seemed possible to separate molybdenum and tungsten in this way from iron and vanadium, with the subsequent determination of molybdenum and tungsten by the Allen and Hamilton method, and vanadium by any one of several methods (Sandell, 1950).

The Reactions of Molybdenum, Tungsten, and Vanadium with Cation-exchange Resins

Molybdenum ^{VI} is retained by a sulphonic resin in the hydrogen form, either by precipitation as molybdic acid (Klement, 1952), or by sorption as the molybdenyl ^{VI} cation (Alimarin and Medvedeva, 1955a). This molybdenum can be removed as molybdate or as a negatively charged complex without removing the cations, by washing the resin with, for example, sodium hydroxide (Lur'e and Filippova, 1947), ammonium thiocyanate (Crouthamel and Johnson, 1954), or sodium ammonium hydrogen phosphate (Matsuo and Iwase, 1955). When an ammonium form of resin is used (Samuelson, 1953, pp. 136, 141-2), or if, when a hydrogen form is employed the molybdenum is complexed with citric acid (Klement, 1952) or hydrogen peroxide (Alimarin and Medve-

deva, 1955a), the molybednum passes through. Even under the reducing conditions of excess sulphur dioxide to reduce vanadium V to vanadium IV, molybdenum complexed with citric acid is not retained by a hydrogen form of resin (Klement, 1952).

Tungsten VI acts in a manner similar to molybdenum VI. It is held by a sulphonic resin in the hydrogen form (Samuelson, 1953, pp. 136, 141-2), and is washed out with sodium hydroxide (Lur'e and Filippova, 1947). Its retention can be prevented by using an ammonium form of resin (Samuelson, 1953, pp. 136, 141-2), or by complexing with hydrogen peroxide if a hydrogen form (Alimarin and Medvedeva, 1955a) is used.

Vanadate passes through an ammonium, but not through a hydrogen form of resin (Samuelson, 1953, pp. 136, 141-2)3. This is due to reduction by the hydrogen form, of vanadate to vanadyl ions (e.g., Devlin, *et al.*, 1949), which are then sorbed. In acid medium, vanadium V is sorbed also as vanadyl V ion (Salmon and Tietze, 1952), and it is suggented that reduction to vanadium IV follows rather than precedes adsorption (Salmon and Tietze, 1952). The extent of the retention of vanadium V by a hydrogen form of resin depends on a number of factors such as the concentration of other ions, e.g., hydrogen and tungstate (Matsuo and Iwase, 1955), and the type of resin (Salmon and Tietze, 1952). Where vanadate is complexed with hydrogen peroxide, no vanadium is retained (Alimarin and Medvedeva, 1955a). However, vanadium IV is always quantitatively adsorbed (e.g., Klement, 1952).

A Possible Procedure

From a consideration of these facts regarding the actions of molybdenum, tungsten, and vanadium towards sulphonic resins, the most promising method of separating molybdenum and tungsten from iron and vanadium appeared to be that of Klement (1952). In this procedure, molybdenum complexed with citric acid in dilute mineral acid and passed through a hydrogen form of resin was quantitatively separated from iron, copper, lead, nickel, chromium, and vanadium IV. (The concentrations of citric and hydrochloric acids necessary for the separation of iron from molybdenum have since been more critically examined by Alimarin and Medvedeva (1955b)). Results < 25 mg Mo were stated to be unreliable, but this seemed due to the gravimetric determination rather than the separation stage.

Confirmation of Procedure

Non-Retention of Molybdenum and Tungsten by Resin

Preliminary experiments showed that micro-amounts ($\leq 20\ \mu g$) of both molybdenum and tungsten in 0·1M HCl containing either 0·2% or 2·0% of citric acid (H_3Ci) passed quantitatively through a column of a hydrogen saturated sulphonic resin. A $1{\cdot}3 \times 7$ cm column of Zeokarb 225 (particle size 0·125 to 0·25 mm) was used.

Retention of Vanadium by Resin

Only from 10 to 20 μg V was retained by the resin from 100 μg as vanadate in 0·1M HCl containing 0·2% H_3Ci. Increasing the citric acid concentration to 1% gave complete retention for amounts of vanadium up to 1,000 μg. The retention was not diminished when ferric iron in amount 5,000 times that of vanadium was added, but was reduced to $< 5\%$ when the solution contained 0·15% H_2O_2 (cf. Alimarin and Medvedeva, 1955a).

It was further observed that, although no reduction of vanadium ^{V} took place in cold solutions of citric acid, there was evidently complete reduction (as evidenced by the change in colour to a pure blue) on heating to boiling. This could not be checked volumetrically with permanganate, as the permanganate was itself reduced. However, the completeness of the reduction was confirmed by showing the equality of the absorption at 760 mμ of solutions of 150 mg V reduced (a) by sulphur dioxide (Santini, *et al.*, 1952), and (b) by heating in 1% H_3Ci. Furthermore, the formaldoxime complex of vanadium ^{IV} (Tanaka, 1954) was quantitatively formed equally rapidly from solutions of vanadium ^{V} reduced with either sodium metabisulphite or heated citric acid. Since the greatest amount of vanadium from a 5 g soil sample would be in the region of only 1·5 mg, the preliminary reduction with sulphur dioxide used by Klement (1952) was dispensed with.

The citric acid, then, has the dual function of reducing the vanadium ^{V} to vanadium ^{IV}, thus ensuring its complete adsorption on the resin column, and of complexing the molybdenum and tungsten, ensuring their non-retention on the column.

Elution of Vanadium from Resin

Proceeding from the observation that $> 95\%$ of the vanadium ^{V} passed through the column when the solution contained 0·15% H_2O_2, and assuming that the vanadium ^{IV} on the column would be oxidized to vanadium ^{V}, it was found that vanadium was, in fact, efficiently eluted from the resin as the orange per-acid by 0·15% H_2O_2. About 10 to 50 μg Fe, and approximately 10 μg Ti were eluted with the vanadium from a column holding 25 mg Fe and 10 mg Ti.

Tentative Procedure

The solution of molybdenum, tungsten, and vanadium in 0·1M HCl containing 1% H_3Ci, after heating to boiling was passed into a column of a cation-exchange resin in the hydrogen form. The effluent, containing molybdenum and tungsten, was boiled down to a small volume and made strongly acid with sulphuric acid. In this condition molybdenum only, and not tungsten, was complexed with dithiol, and extracted into petroleum ether. After evaporating off most of the sulphuric acid, the tungsten complex with dithiol was formed, and

extracted into petroleum ether. The vanadium, eluted from the column free of other cations by 0·15% H_2O_2, was determined by the phosphotungstate method as described by Sandell (1950). Measurements of the absorbances of the molybdenum and tungsten dithiol complexes in petroleum ether were made in the 50 mm microcuvettes of the Coleman model 14 Universal spectrophotometer. The absorbance of the vanadium phosphotungstate was measured in a 13 mm cuvette.

Interfering Elements

Molybdenum and Tungsten by Dithiol

The only elements in the soil that would interfere seriously in the dithiol methods for molybdenum and tungsten are iron, copper, and tin (Allen and Hamilton, 1952, Williams, 1955, Piper and Beckwith, 1948). The mutual interference of molybdenum and tungsten is negligible when the molybdenum complex alone is formed in, and extracted from, strong sulphuric acid. Allen and Hamilton (1952) have stated that 10 μg Mo can be estimated in the presence of 500 μg W with an error of $< 1\%$. Fortunately, it would be expected that all of the iron, copper, and tin would be retained on the resin column. Klement (1952) has quantitatively retained iron and copper in dilute hydrochloric-citric acids on a cation-exchange resin, while Lur'e and Filippova (Samuelson, 1953, p. 152) have retained tin from 0·6M HCl.

The maximum amounts of copper, and tin that have been found in New Zealand soils (Mr N. Wells, pers. comm.) are 250 p.p.m., and 30 p.p.m. respectively—corresponding in a 5 g sample to 1·25 mg Cu and 150 μg Sn. To test for interference, iron was added at an arbitrarily large amount of 100 mg, together with 1·25 mg Cu, and 150 μg Sn. It was found that with a citric acid concentration of2%, some tin passed through the column and increased 5 μg Mo to apparent amount of 5·3 μg. Tin gives no absorbance on its own, it merely enhances the absorbance of the molybdenum complex (Piper and Beckwith, 1948). Negligible amounts of tin passed through the column at a citric acid concentration of 1%, and caused no interference. With greater amounts of tin, the amount of citric acid may need to be lowered further.

Small amounts of platinum are dissolved by iron in hydrochloric acid from platinum ware used in the fusion or hydrofluoric acid treatment of soil samples. This platinum interferes in the molybdenum determination by dithiol (Clark and Axley, 1955), but the manner in which the interferences can be avoided will be discussed later.

Molybdenum

Solutions, mixed as indicated in Table 1, of molybdenum, iron, copper, tin, and vanadium in 0·1M HCl containing 1% H_3Ci were heated to boiling and passed into the resin column. After the column had been washed with water, the effluent was evaporated to a small

volume in a beaker, and transferred to a glass-stoppered test tube. It was then boiled with nitric, perchloric, and sulphuric acids, until fumes of sulphuric acid were evolved, in order to oxidize the citric acid completely. The solution was made 12N with respect to sulphuric acid, and the molybdenum dithiol complex was formed, extracted, and measured, as in the method of Allen and Hamilton (1952) following Piper and Beckwith (1948). The recoveries of molybdenum are shown in Table 1.

TABLE 1.—Molybdenum Recovered from Iron, Copper, Tin, and Vanadium.

Elements Added (μg)					Recovered				Average
Mo	Fe	Cu	Sn	V	Mo				Mo
5	—	—	—	—	4·98	4·99	4·98	4·98	4·98
—	100,000	1,250	150	1,000		0·00	0·01		0·01
5	100,000	1,250	150	1,000	4·99	4·97	4·99	5·00	4·99

TUNGSTEN

The solution of tungsten with the other four elements was passed into the resin column as for molybdenum. The effluent was boiled down first in a beaker, and then in a test tube to 0·5 ml H_2SO_4. From this point the procedure of Allen and Hamilton was followed viz., the pH was adjusted to 0·5 to 2·0, and the tungsten complex was formed, extracted, and measured. The recoveries of tungsten are given in Table 2.

TABLE 2.—Tungsten Recovered from Iron, Copper, Tin, and Vanadium.

Elements Added (μg)					Recovered			Average
W	Fe	Cu	Sn	V	W			W
5	—	—	—	—	5·01	4·93	4·96	4·97
—	100,000	1,250	150	1,000		0·00	— 0·02	— 0·01
5	100,000	1,250	150	1,000		5·00	4·97	4·99

Vanadium by Phosphotungstate

Since very small amounts of titanium were eluted with the vanadium by the hydrogen peroxide, the phosphotungstate method—which is less sensitive to titanium interference—was chosen for the vanadium determination rather than the peroxide. However, where the proportion of titanium to vanadium is sufficiently small, measuring vanadium as the peroxide complex would be quicker. Molybdenum, the only other interfering element, has previously been separated.

The ions occurring in sufficient quantities in the soil to interfere in the phosphotungstate method for vanadium are potassium, ammonium,

iron, and titanium, with possibly chromium, and zirconium (Wright and Mellon, 1937). As ammonium and potassium would not be eluted to any large extent by hydrogen peroxide, their effect was not ascertained. The highest concentrations of titanium, chromium, and zirconium that have been found in New Zealand soils by Mr N. Wells (pers. comm.) are 10,000 p.p.m., 300 p.p.m., and 1,200 p.p.m.—which correspond in a 5 g sample to 50 mg, 1·5 mg, and 6 mg respectively. Solutions of these amounts of the elements, together with iron and vanadium, were mixed as in Table 3 to test for interference. The zirconium stock solution was made up in 1% H_3Ci, with the pH adjusted to 4·0 with ammonia (Brown and Rieman, 1952). At lower pH values the zirconium becomes colloidal (Brown and Rieman, 1952, Ayres, 1947), and passes completely through a resin column saturated with hydrogen (Ayres, 1947).

After the mixed solutions had been passed through the column, and the remaining liquid washed out with water, the adsorbed vanadium was eluted with 0·15% H_2O_2. The vanadium complex in this solution was exceptionally stable. If it was not destroyed completely by boiling until fumes from 0·5 ml of H_2SO_4 appeared, then low values for vanadium were obtained. Following the sulphuric acid treatment, phosphoric acid and sodium tungstate were added in the concentrations given by Sandell (1950) to develop the yellow complex. The recoveries of vanadium are given in Table 3. Sometimes when large amounts of iron were present (held at the top of the column), the hydrogen peroxide was decomposed, evolving bubbles of oxygen, which in turn caused an uneven flow of peroxide through the column. Recoveries of only 96 to 97% V were obtained unless the bubbles were removed by shaking the top part of the column with a little water.

Table 3.—Vanadium Recovered from Iron, Titanium, Chromium, and Zirconium.

Elements Added (μg)					Recovered			Average
V	Fe	Ti	Cr	Zr	V			V
100	—	—	—	—	100·3	99·7		100·0
—	100,000	50,000	1,500	—	1·0	−1·0	0·0	−1·0	−0·3
100	100,000	50,000	1,500	—	100·3	99·2		99·8
—	—	—	—	6,000	−1·0	1·0	1·0		0·3
100	—	—	—	6,000	101·1	100·0	100·0		100·2
						100·6	99·4	

Analysis of Soils and Fertilizers

Oxalate Extracts and Fertilizers

Reproducible results were obtained in the analysis of Grigg's (1953) oxalate extract of soils. After the extract had been evaporated and ignited, any remaining organic material was destroyed with perchloric acid, and the solution evaporated to dryness at a low temperature.

The solid was dissolved in hydrochloric and citric acids and diluted to give a final concentration of 0·1M HCl and 1% H_3Ci. From this point the analysis was continued as previously outlined. The last three extracts in Table 4 contained a large amount of iron.

TABLE 4.—Molybdenum, Tungsten, and Vanadium in Oxalate Extracts.

Soil Type	Depth (in.)	Mo (p.p.m.)		W (p.p.m.)		V (p.p.m.)	
Warepa silt loam	0 to 1	0·071	0·065	0·023	0·024	4·6	5·2
Warepa silt loam	1 to 3	0·062	0·061	0·024	0·020	5·0	4·9
Warepa silt loam (sodium molybdate applied twice at 8 oz/acre)	0 to 3	0·495	0·497	0·015	0·015	*	
Whangamata gravelly sandy loam	0 to 3	0·594	0·595	0·038	0·038	*	
Pongakawa peaty loam	0 to 3	0·920	0·912	0·051	0·049	*	
Kereone silt loam	0 to 3	0·565	0·559	0·089	0·077	*	

*Not analysed for vanadium.

The method was also applied successfully to phosphatic fertilizers (as exemplified in Table 5), and steel. One gm of fertilizer was heated with hydrochloric, nitric, and perchloric acids, and then treated with hydrofluoric acid. The solution was evaporated to dryness, and the residue taken up in hydrochloric and citric acids.

TABLE 5.—Molybdenum, Tungsten, and Vanadium in Fertilizers.

Sample	Mo (p.p.m.)		W (p.p.m.)		V (p.p.m.)	
N.Z. Dunite-Nauru rock phosphate fusion	0·23	0·21	0·32	0·28	37	37
Japanese fused magnesium phosphate	6·8	6·8	0·67	0·33	89	90
Mono-calcium phosphate	$<0·02$	$<0·02$	0·12	0·12	8·5	8·5

Total Amounts

SEPARATION OF MOLYBDENUM AND TUNGSTEN BY DITHIOL

Total analyses based on Perrin's method (1946) were made. The soil was ashed at 450° C overnight to remove organic material, treated with hydrofluoric acid to remove silicon, and boiled with concentrated hydrochloric acid. After evaporating the hydrochloric acid to dryness, the residue was dissolved in hydrochloric and citric acids, the solution was diluted to give 60 ml of 0·1M HCl and 1% H_3Ci, and the molybdenum, tungsten, and vanadium were determined. Good results were obtained for vanadium. Some duplicates for molybdenum were in good agreement, while others were not. The molybdenum dithiol complex had been extracted from a small volume of 12 ml to minimise

the amount of sulphuric acid to be evaporated off in the tungsten determination. When it was extracted from a larger volume, 25 ml, then satisfactory agreement was achieved. Most of the tungsten figures were very low, but when above the order of analytical error, were in poor agreement.

The lower results for molybdenum, and more particularly for tungsten, were attributed to the effects of the relatively large amounts of aluminium and titanium that were found to pass through the cation-exchange resin column in the citric acid solution. When the effluent from the resin column was concentrated to give 10 ml of 12N H_2SO_4 for the molybdenum determination, a white precipitate, presumably of titanyl sulphate, was formed. Some molybdenum or tungsten may have been sorbed on this precipitate. Also, since much solid was present, it was very difficult to estimate when the sulphuric acid had been evaporated down to 0·5 ml prior to the tungsten determination. Furthermore, the salt was incompletely dissolved on boiling with water. More solid remained undissolved after boiling off an excess of ammonia added, and redissolving the precipitate formed with dilute sulphuric acid (aluminium hydroxide becomes less soluble after boiling). The high salt concentration, the insoluble residue, and the possibility of the pH being outside the correct range, appeared to be the main factors in the low values for tungsten. A further separation of molybdenum and tungsten from aluminium and titanium was therefore necessary.

Jeffery (1956) separated molybdenum and tungsten from a number of ions, including aluminium and titanium, by a four-fold extraction of the α–benzoinoxime complexes of molybdenum and tungsten into chloroform. However, this method still involves the careful fuming off of sulphuric acid in the determination of tungsten following that of molybdenum. The amount of sulphuric acid at 0·5 ml is fairly critical: if much more is present, then the higher salt concentration to which it gives rise will produce low results; while if the solution is evaporated to dryness low values will again be obtained.

Separation of Molybdenum and Tungsten by Anion-Exchange

The anion-exchange studies of Kraus, *et al.* (1954, 1955) indicated the possibility of a separation of molybdenum and tungsten from aluminium and titanium, and from each other. From 9M HCl, molybdenum and tungsten are sorbed (Kraus, *et al.*, 1955), while aluminium and titanium are not (Kraus, *et al.*, 1954), by an anion-exchange resin. Tungsten, but not molybdenum is eluted from the column with 9M HCl–1M HF (Kraus, *et al.*, 1955). Molybdenum is eluted with 1M HCl (Kraus, *et al.*, 1955). This separation was tried, and proved effective.

The chromatographic separations were made with a 15×1 cm column of 120 to 200 mesh particle size of Amberlite 400. Fifty micrograms of molybdenum and 40 μg W, separately and together, were sorbed on to the column from 9M HCl, and eluted with 9M HCl–1M HF (for tungsten) and 1M HCl (for molybdenum). Substantially

the same elution curves as those of Kraus, Nelson, and Moore (1955) were obtained, and with the recoveries of 100·0 to 100·7% of the amounts taken. Since the effluent from the cation-exchange resin column contains citric and sulphuric acids as well as hydrochloric acid, the effect of these acids on the sorption of molybdenum and tungsten from C.B.P. hydrochloric acid was tested. Molybdenum and tungsten are eluted by 6M HCl–1M H_3Ci in approximately four column volumes (Mr J. C. B. White, pers. comm.). Thus, it was desirable to keep the volume of solution small from which the molybdenum and tungsten were sorbed to avoid their passage through the column, and also to shorten the time taken for analysis. A solution containing 50 μg Mo, 40 μg W, 1 g H_3Ci, 1·2 ml conc. H_2SO_4, and 10 ml conc. HCl was evaporated down to 5 ml, and passed through the column. The column was washed with $2\frac{1}{2}$ column volumes of 9M HCl. No molybdenum or tungsten was detected ($< 0{\cdot}4$ μg) in the effluent.

Kraus, Nelson, and Smith (1954) found titanium and aluminium to pass through a column on washing with $2\frac{1}{2}$ column volumes of 9M HCl, and 7M HCl respectively. Aluminium was not sorbed at any strength of hydrochloric acid. It was confirmed that both 10 to 20 mg Ti, and 1 mg Al were eluted in $2\frac{1}{2}$ column volumes of 9M HCl after being introduced into the column in 5 ml of the mixture of citric, sulphuric, and hydrochloric acids used for molybdenum and tungsten.

As small, but sufficient amounts of platinium to interfere in the dithiol method for molybdenum are dissolved under some circumstances from platinum ware (Clark and Axley, 1955), its behaviour in the separation scheme for molybdenum and tungsten was briefly investigated. It is sorbed strongly from solutions having concentrations of hydrochloric acid from 0·1M to 11·6M (Kraus, *et al.*, 1954). It was found that 800 μg Pt was strongly sorbed from 5 ml of the mixture of citric, sulphuric, and hydrochloric acids. It was not detected ($< 0{\cdot}5$ μg) in the effluents from consecutive elution with $2\frac{1}{2}$ column volumes of 9M HCl, 8 column volumes of 9M HCl–1M HF, and 8 column volumes of 1M HCl. Hence, with this separation, platinum will not interfere in the dithiol determinations of molybdenum or tungsten.

When the anion-exchange separation of molybdenum and tungsten was used in place of the dithiol separation, very satisfactory total analyses were achieved, as illustrated in Table 6.

Recoveries of the three elements added to four soils were also made. The solutions were added to the soil before and after ignition. In the former case the sample was evaporated to dryness on a boiling water bath before igniting in a muffle furnace. Compared with the addition after ignition, the results for molybdenum and tungsten are lower, and for tungsten and vanadium more variable. Losses during the ignition more probably occurred by adsorption on the sides of the silica beaker than by volatilization. The recoveries shown in Table 7 can be taken as satisfactory.

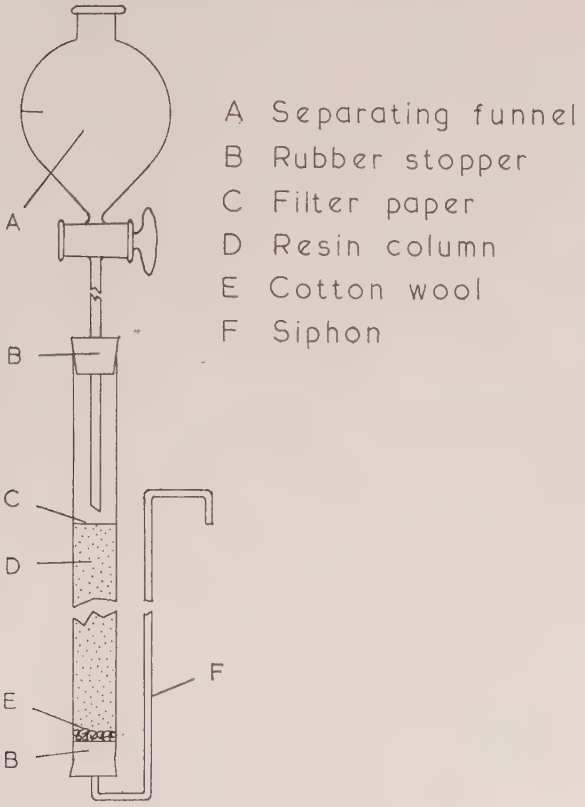

FIG. 1.

ANALYTICAL METHOD

Special Apparatus and Reagents

RESIN COLUMNS

Make up a column (Fig. 1) of a strongly acidic cation-exchange resin of particle size in the approximate range 0·125 to 0·25 mm. Two sizes (according to sample size) have been found convenient—1·3 × 7 cm and 1·5 × 20 cm. A narrow siphon prevents the column from draining dry. The liquid reservoir is a separating funnel marked at 60 ml and 120 ml, and fitted into the glass tubing containing the column with a rubber stopper as in the figure. To keep a constant and sufficient pressure above the column as the solution passes through, the funnel has a long, narrow stem that readily fills with liquid. The flow rate is controlled by the stopcock. Regenerate with 3 to 4M HCl.

Make up a 1 × 15 cm column (Fig. 2) of a strongly basic anion-exchange resin having a particle size range of 0·125 to 0·076 mm, or

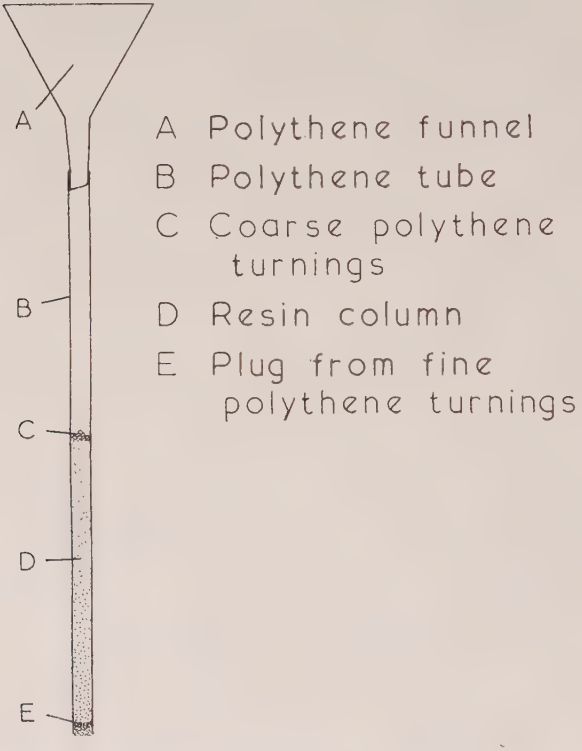

FIG. 2.

finer. The column is contained in a 1 × 30 cm polythene tube plugged at the bottom, and fitted tightly at the top with an 8 cm polythene funnel to contain the liquid passing through the column. A cotton wool plug disintegrates in the strong hydrochloric acid, but a very satisfactory plug can be made from fine polythene turnings formed on a lathe. Glass tubing, etc. is precluded from use by the hydrofluoric acid solutions used. No siphon is necessary because the fine column does not dry out and crack. However, it is advisable to wash the column with strong, say 9M HCl if it is to be kept unused for more than 24 hr, as otherwise it will dry out.

PETROLEUM ETHER, BOILING RANGE 100° TO 120° C

Purify by shaking with concentrated sulphuric acid followed by water.

DITHIOL, 0·2%

Dissolve 1 g of dithiol, melted by warming the ampoule to 30° to 35° C, in approximately 100 ml of water containing 5 g NaOH

Table 6.—Total Molybdenum, Tungsten, and Vanadium.

Soil Type	Depth (in.)	Parent Material	Mo (p.p.m.)	Mo (Av.)	W (p.p.m.)	W (Av.)	V (p.p.m.)	V (Av.)
Korokoro silt loam	0 to 3	Greywacke	0·70 0·76	0·73	1·47 1·59	1·53	83·0 82·7	82·9
Warepa silt loam	0 to 1	Loess from schist	0·31 0·32 0·31	0·31	1·26 1·28 1·25	1·26	79·7 80·1 80·2 81·0 81·6	80·5
Warepa silt loam	1 to 3	Loess from schist	0·34 0·27 0·33	0·31	1·35 1·34 1·23	1·31	78·3 79·1 80·2 81·1 82·5	80·2
Riponui sandy clay loam	0 to 3	Sandstone	0·79 0·74 0·75	0·76	0·65 0·67	0·66	235 235 240	237
Te Kopuru sand	0 to 3	Slightly consolidated sandstone	0·93 0·90 0·95	0·93	1·09 1·04 1·03	1·05	9·6 10·2 10·3 11·1	10·3
Mapua sandy loam	0 to 3	Moutere gravel	0·19 0·24	0·22	0·57 0·58	0·58	26·3 27·1	26·7
Taupo shallow sandy silt	0 to 3	Taupo on Tirau ash	1·25 1·24	1·25	1·22 1·20	1·21	25·8 24·3	25·1
Kereone silt loam	0 to 3	Tirau ash	1·48 1·49	1·49	1·67 1·71	1·69	77·5 76·5	77·0
Hamilton clay loam	0 to 3	Hamilton ash	1·39 1·48	1·44	1·74 1·77	1·76	107 106	107
Rangiuru clay†	0 to 3	Andesite	1·09 1·01 1·14	1·08	0·56 0·54 0·52	0·54	412 413 417	414
Awapuku clay loam	0 to 3	Andesitic basalt and andesite	0·79 0·78 0·88	0·82	0·58 0·52 0·49	0·53	279 285 283	282
Whatoro clay loam	0 to 3	Andesitic basalt	2·45 2·49	2·47	2·44 2·37	2·41	430 429	430
Whatatiri clay loam	0 to 3	Basalt	3·16 3·21	3·19	1·44 1·42	1·43	184 178	181
Rukuhia peat	0 to 3	Peat	0·42 0·48	0·45	0·38 0·39	0·39	15·6 19·3	17·5
Pongakawa peaty loam	0 to 3	Peat, Kaharoa ash and alluvium	2·09 2·19	2·14	0·57 0·61	0·59	34·8 34·7	34·8
Kaitaia clay loam	0 to 3	Alluvium from sedimentary rocks and andesitic basalt	0·71 0·73	0·72	0·73 0·71	0·72	209 211	210
Arapohue clay	0 to 3	Argillaceous limestone	0·46 0·45	0·46	1·19 1·18	1·19	79·2 75·7*	77·5
Waiareka clay loam	0 to 3	Basalt over limestone	0·67 0·68	0·68	1·00 0·99	1·00	102 100	101

†Fusion analysis.
*Slightly low.

Table 7.—Recovery of Molybdenum, Tungsten, and Vanadium.

Addition Before Ignition

Sample	Mo (μg)				W (μg)				V (μg)			
	Added	Calculated	Found	Difference %	Added	Calculated	Found	Difference %	Added	Calculated	Found	Difference %
Warepa silt loam	4·85	5·47	5·44	−0·6	4·80	7·33	6·83	−6·8	100	262	278	+6·1
Pongakawa peaty loam	1·94	5·17	5·03	−2·7	4·80	5·69	5·40	−5·1	100	152	150	−1·3
Riponui sandy clay loam	4·85	5·59	5·31	−5·0	4·80	5·45	5·47	+0·4	100	335	350	+4·5
Whatatiri clay loam	1·94	5·34	5·06	−5·2	4·80	6·32	5·95	−5·9	100	292	295	−1·5
Addition After Ignition												
Warepa silt loam	4·85	5·45	5·54	+1·7	4·80	7·25	7·10	−2·1	100	257	263	+2·3
Pongakawa peaty loam	1·94	4·88	4·86	−0·4	4·80	5·61	5·47	−2·5	100	148	150	+1·4
Riponui sandy clay loam	4·85	5·60	5·43	−3·0	4·80	5·46	5·37	−1·6	100	338	343	+1·5
Whatatiri clay loam	1·94	4·92	5·03	+2·2	4·80	6·13	5·92	−3·4	100	269	265	−1·5

(dithiol dissolves much more rapidly in 5 to 8% than 1% NaOH). Dilute to 500 ml, and stir in about 8 ml of thioglycollic acid until a faint precipitate forms. Immediately seal in 100 ml polythene bottles and store in a refrigerator.

Detailed Procedure (Total)

DIGESTION OF SOIL SAMPLE

Grind the sample to pass a 120 mesh sieve. Ash from 1 to 5 g of soil in a platinum basin (or 100 ml tall form silica beaker) overnight (16 hr) in a muffle furnace at 450° to 475° C. Add a few millimetres of water, 10 ml of 40% HF, 0·5 ml of conc. H_2SO_4, and mix with a small strip of polythene. Heat on a water bath at about 80° C and evaporate down to dryness to remove silicon. (A minimum amount of sulphuric acid is added to avoid distilling off the excess at a high temperature, with the the possible formation of insoluble compounds.) If some silica remains, evaporate down again with hydrofluoric acid. Dissolve the residue by boiling with 10 ml of conc. HCl. This treatment will very likely dissolve a little platinum that will interfere in the molybdenum determination if the anion-exchange separation is not used. In the latter case, transfer the residue to a beaker before boiling. Evaporate to dryness on a water bath to prevent bumping and loss of solubility of the solid material.

SEPARATION OF VANADIUM

Heat the residue with 1 ml of C.B.P. HCl, and 4 to 5 ml of water. Add approximately 25 ml of water, then 2 ml of 50% H_3Ci, and heat to boiling. If the citric acid is added before diluting, insoluble citrates sometimes form. Filter the solution through a 9 cm Whatman No. 42 filter paper into the separating funnel above the cation-exchange resin column. Wash the paper with hot water. Dilute the filtrate with a strong jet of water from a wash bottle to give a well-mixed solution of about 60 ml. If a large sample was taken it may be necessary to dissolve the solid in twice the volume. Open the stopcock, and pass the solution through the column at 2 to 3 ml per minute into a 250 ml beaker. When the solution has drained to the top of the column, wash through with 50 ml of water. Add 5 ml of conc. HCl to the effluent.

Elute the vanadium from the cation-exchange resin column with 100 ml of 0·15% (0·5 volume) H_2O_2, followed by 25 ml of water, into a 250 ml beaker. Add 0·5 ml of conc. H_2SO_4, a few drops of perchloric acid, and boil to a small volume. If the peroxide solution is strongly coloured, indicating an amount of vanadium > 400 to 500 μg, dilute in a volumetric flask and take an appropriate aliquot. Wash into a 6 in. x 1 in. glass-stoppered test tube containing a glass ball, and boil down until fumes of perchloric acid appear. Allow to cool, add 2·5 ml of 1:2 H_3PO_4, 1·5 ml of 0·5 M Na_2WO_4, a little water, and boil. Measure the absorbance in a 10 mm cuvette at 400mμ after diluting to 25 ml.

Separation of Molybdenum and Tungsten

At first boil the molybdenum and tungsten solution in the 250 ml beaker, and later evaporate down more carefully, to about 5 ml (from 3 to 9 ml have been used without adverse effects). Pass this solution through the anion-exchange resin column and collect the effluent in a small beaker. Rinse the 250 ml beaker with two portions of 10 ml of 9M HCl and pass these successively through the column when the first solution has drained to the top. Discard the effluent.

Elute the tungsten with 70 ml of 9M HCl–1M HF into a platinum or polythene basin. Add 1·5 ml of 10N H_2SO_4 and evaporate down to sulphuric acid on a water bath. Transfer to a 6 in. x 1 in. pyrex glass-stoppered test tube, add 1 ml of $FeSO_4$ (1 mg Fe/ml), and dilute to 25 ml. After shaking with 4·5 ml of 0·2% dithiol solution, place the tubes in a water bath at 90° to 95° C for half an hour. Cool to room temperature, and extract the dithiol complex into 10 ml of petroleum ether by shaking vigorously for three periods of 1½ min. Separate the phases, and centrifuge or filter the water droplets out of the ether. Measure the absorbance of the ether at 630 mμ in a 50 mm microcuvette. Alternatively, the tungsten may be determined directly in the 9M HCl–1M HF solution following the method of Bagshawe and Truman (1947). In qualitative tests, the hydrofluoric acid did not prevent the formation of the tungsten complex in 9M HCl.

Elute the molybdenum from the anion-exchange column with 70 ml of 1M HCl into a 100 ml separating funnel. Add 1 ml of $FeSO_4$ (1 mgm Fe/ml), 20 ml of conc. H_2SO_4, 2 ml of 0·2% dithiol solution, shake, and stand for 1hr. Shake vigorously for three periods of 1½ min. with 10 ml of petroleum ether to extract the molybdenum complex. Continue as with the tungsten complex except that the absorbance is measured at 680 mμ.

Alternative Separation of Molybdenum and Tungsten

When the amounts of titanium and aluminium are small, the procedure of Allen and Hamilton can be followed. Boil the effluent from the cation-exchange resin column containing molybdenum and tungsten to a small volume with 1 ml of $FeSO_4$ (1 mgm Fe/ml), 5 ml of conc. HNO_3, a few drops of perchloric acid, and 4 ml of conc. H_2SO_4. Transfer to a 6 in. x 1 in. pyrex glass-stoppered test tube, and boil. As the nitric acid concentrates, the citric acid is oxidised. If charring commences, add more nitric acid until all the citric acid has been oxidised. Continue to boil for a few minutes after all the perchloric acid has distilled off. After adding a little water, boil again to dissolve the salt present, cool, dilute to 10 ml, and cool again. Add 2 ml of 0·2% dithiol solution, and stand at room temperature (12° to 20° C) for 1 hr. Extract and measure the molybdenum complex as previously described. Evaporate the aqueous phase on a hotplate to about 0·5 ml of conc. H_2SO_4 in a small beaker. Wash into a 6 in. x 1 in. pyrex glass-stoppered test tube, neutralize with ammonia—as indicated

by the appearance of ferric hydroxide—and boil off the excess. Add 1·5 ml of 10N H_2SO_4, boil to dissolve the precipitate, and dilute to 25 ml. Form and measure the tungsten dithiol complex as previously described.

REMARKS

Under the conditions tested for pure solutions, and where known amounts have been added to soil samples, there is a satisfactory recovery of all three elements. The duplicate analyses of soil extracts and fertilizers are in reasonable agreement, and the total amounts of molybdenum and vanadium found are within the same ranges as those found by other investigators. The values reported for tungsten are of the same order as for molybdenum (as predicted from Goldschmidt's ratio), but lie within a more restricted range.

A few samples were analysed for iron to find the ratios of iron to molybdenum, and to tungsten that are likely to be encountered. As shown in Table 8 the proportion varies from 2,000 to 200,000, which is very high.

TABLE 8.—Proportion of Iron to Molybdenum and Tungsten.

Soil Type	Fe (p.p.m.)	Fe/Mo	Fe/W
Whatatiri clay loam	77,500	24,000	54,000
Rangiuru clay	104,000	96,000	193,000
Te Kopuru sand	1,900	2,000	1,800
Warepa silt loam	28,000	90,000	22,000
Pongakawa peaty loam	44,500	2,100	75,000

In one soil, Rangiuru clay, there remained a residue of 200 mg from a 3 g sample after treating with hydrofluoric and hydrochloric acids. This dissolved only after fusing with sodium carbonate. Two grams of sodium carbonate were fused with 2 and 1 g of the soil, the melt dissolved with dilute hydrochloric acid, and the solution treated with hydrofluoric acid, etc. following the normal procedure. With the 1:1 ratio of sodium carbonate to sample, the melt dissolved completely in acid, but not so readily as the 2:1 mixture. Clark and Axley (1955) used a 2:1 ratio for a large number of soils without any difficulties, so it is probably a good working value. When an appreciabale residue is found in the normal course of analysis, fuse the filter paper and residue with 1 g of Na_2CO_3 in a platinum crucible, dissolve in dilute hydrochloric acid, add to the solution of hydrochloric acid already obtained, and continue as usual.

The separation used not only makes possible the analysis of material other than soils, but also the analysis of other ions remaining on the resin column, e.g., iron, copper, cobalt, etc. Iron and copper have been determined in this way. If the column is uniform, a semi-quantitative measurement of iron can be made as a red band on treat-

ing with dilute thiocyanate (Crouthamel and Johnson, 1954). Any titanium remaining on the cation-exchange column is revealed as an orange band when the peroxide passes through.

Since the lower limit of measurement of molybdenum and tungsten in a 5 g sample is of the order of 0·02 to 0·03 p.p.m., the method can be used to analyse plant samples for molybdenum and tungsten. However, a more sensitive reagent than phosphotungstate (lower limit of measurement about 0·4 p.p.m. V) is necessary to determine the much smaller amounts of vanadium present. This determination will be the subject of a later paper.

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PODOCARPUS SPICATUS HEARTWOOD EXTRACTIVES

By H. V. BREWERTON, Dominion Laboratory, Department of Scientific and Industrial Research, Wellington

(Received for publication, 7 March 1958)

Summary

The heartwood extractives of *Podocarpus spicatus* (matai) have been examined and four compounds have been isolated in good yields. It has been ascertained that no podocarpic acid is present in the heartwood. No matairesinol, totarol, nor ferruginol was found. A simple test to distinguish between the heartwood and sapwood of matai is given.

INTRODUCTION

The heart shakes resin of the New Zealand native timber tree matai (*Podocarpus spicatus*) was found by Easterfield and Bee (1910) to be predominantly matairesinol. The molecular structure of matairesinol was determined as a lactonic lignan by Haworth and Richardson (1935) and Briggs *et al.* (1935) who also noted traces of the structurally related conidendrin and another compound (m.p. 212° C) in the heart shakes resin.

Brandt and Thomas (1952) have recorded that the structurally related diterpenes podocarpic acid, totarol, and ferruginol are characteristic of timbers of the Podocarpus genus previously studied, thereby drawing attention to the anomalous nature of the heart shakes of matai. However, it was noted by these authors that the heartwood extractives of this timber had not been investigated.

This paper describes a study of the acetone extractives of matai heartwood including a search for podocarpic acid, totarol, and ferruginol.

EXPERIMENTAL

All percentage yields quoted are based on the oven-dry weight of heartwood.

Heartwood grounds having a dry weight of 282g were extracted with acetone continuously for 7 hours. The extract in 17·6% yield was dried under vacuum, finely powdered, and exhaustively extracted with ether.

Fractional crystallization of the ether extract yielded 1·618g of compound I (m.p. 212° C) and 0·578g of compound II (m.p. 252° C). The ether mother liquor was extracted successively with 5% aqueous sodium carbonate and 4% aqueous sodium hydroxide to provide "acidic", "phenolic", and "neutral" fractions in 5·70%, 3·44%, and 0·64% yields respectively.

The "acidic" fraction yielded 0·294g of I by crystallization from ethanol, and 5·472g of compound III (m.p. 226° C) by crystallization from ethanol-benzene. The mother liquors were combined, dried under vacuum and chromatographed in ether on alumina. Elution with ether provided 0·012g of I and 0·661g of III. Elution with 20% (v/v) methanol-ether provided 0·125g of II. Further elution with methanol and acetone gave non-crystalline residues in low yield. The alumina column was exhaustively washed with 4% aqueous sodium hydroxide to yield 2·378g of non-crystalline dark coloured resin. This was taken up in ether and washed with 3% aqueous sodium bicarbonate. The resulting decolourized ether solution yielded a pale yellow resin which crystallized from ethanol-chloroform to yield 0·402g of III. The ultraviolet absorption spectra of all these portions of the "acidic" fraction were examined and showed no trace of podocarpic acid.

The "phenolic" fraction yielded 0·998g of compound IV (m.p. 301° C) by crystallization from ethanol-chloroform. The mother liquor was dried under vacuum and chromatographed in ether on alumina. Elution successively with ether, methanol-ether, methanol, and acetone gave non-crystalline fracations in low yields. The alumina was exhaustively washed with 4% aqueous sodium hydroxide and the washings acidified. The resulting precipitate was predominantly insoluble in ether. This solubility change is consistent with the behaviour of the tannin-like substances encountered in wood extractives. The ether soluble portion crystallized from ethanol-water to yield 1·10g of crude IV.

The "neutral" fraction was an amber coloured oil which would not crystallize. The yield of the fraction was small and work was confined to a search for totarol and ferruginol. The oil (1·79g) was refluxed in acetic anhydride (7ml) with sodium acetate (2g) for two hours. The reaction product was chromatographed on alumina to isolate totaryl and ferruginyl acetates as reported by Brandt and Thomas (1951) for the extractives of *Dacrydium cupressinum*. Neither compound was obtained. A further quantity of "neutral" oil (2·48g), obtained from an additional extraction of matai, was heated (70° to 90° C) with 20% aqueous sodium hydroxide (20ml) and shaken for one hour. On cooling, the liquor was extracted with ether to yield 1·98g of resinous material. The ether extracted liquor was shaken with benzoyl chloride (5ml) for 30 minutes and the reaction mixture was extracted with ether to yield a non-crystallizable oil (0·57g).

Yields and properties of the compounds I to IV are tabulated below.

Compound	I	II	III	IV
Melting point °C	212	252	226	301
Total yield %	0·68	0·25	2·31	0·74
Optical rotation $[\alpha]_D^{20°}$	Nil	+28	+10	Nil
Colour with $FeCl_3$	Green	Green	Purple-brown	Green
Colour with Mg in HCl-methanol	Nil	Orange	Red	Nil

Ultraviolet Absorption Data

	Minima		Maxima		Inflections	
Compound	mμ	$\log E_{1cm}^{1\%}$	mμ	$\log E_{1cm}^{1\%}$	mμ	$\log E_{1cm}^{1\%}$
I	244	2·67	265	2·80		
	289	2·55	304	2·61		
II	250	2·05	285	2·76	320	2·43
III	252	1·89	291	2·76	325	2·31
IV	232	2·74	263	3·14	330	2·31

Discussion

The infrared spectrum of each of the four major compounds extracted from matai heartwood indicates the presence of hydroxyl and aromatic groups and also shows an absorption band between 1640 and 1655 wavenumbers. These compounds are therefore not acids nor lactones and their spectra are reminiscent of those of 5-hydroxyflavanoids (Hergert and Kurth, 1953). Their alkali solubility and positive ferric chloride colour tests show them to be phenols. The acidity of compounds I, II, and III, as shown by their solubility in aqueous sodium carbonate, is in accordance with that of known polyhyroxyflavanoids. Compounds II and III have ultraviolet absorption spectra very similar to that of aromadendrin (Hillis, 1952) and show colour formation on treatment with magnesium powder in methanolic hydrochloric acid in the manner typical of flavanones.

In view of the work of Easterfield and Bee (1910) it was expected that matairesinol would be present in the solvent extract of matai heartwood and that it would occur in the "phenolic" fraction. Prolonged efforts failed to locate either this substance or the closely related conidendrin. The relationship of heartwood extractives to the exudation resin is therefore obscure. The presence in the heartwood of simple lignan precursors of the C_6——C_2 category seems a probable explanation of the origin of the matairesinol exudation resin.

However, the present work has given no indication of the presence of eugenol or similar substances in matai.

The "neutral" portions of the solvent extract of *Podocarpus totara* and of the exudation resin of *Podocarpus ferrugineus* were the predominant fractions in each case and consisted of totarol (Brandt, unpublished) and ferruginol (Brandt and Neubauer, 1939) respectively. The "neutral" fraction of the solvent extract of matai heartwood, however, was less than 4% of the total extract. Only 20% of the fraction was soluble in hot 20% aqueous sodium hydroxide and in this no totarol nor ferruginol was found.

The properties of podocarpic acid are such that, had it been present in the matai heartwood, it would have been detectable under the treatment accorded the "acidic" fraction. No trace of it was found.

The absence of the structurally related diterpenes totarol, ferruginol, and podocarpic acid, together with the differences between their spectral properties and those of the four compounds characterized in this article, confirm that matai has extractives chemically unlike those reported for other Podocarpus timbers (Brandt and Thomas, 1952). However, a more detailed investigation of the extractives of *P. totara* and *P. ferrugineus* is necessary before any question is raised concerning the taxonomical relationship of these timbers.

The high yield of phenolic extractives leads to the provision of a simple test, required in timber preservation work, to distinguish between heartwood and sapwood of matai. When 5% aqueous ferric chloride is applied to a trunk cross-section, a black stain forms almost immediately on the heartwood, a pale green colour characterizes the sapwood and the interface between these is sharply defined.

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MARINE FOULING AT THE PORT OF LYTTELTON

By T. M. SKERMAN, New Zealand Oceanographic Institute, Department of Scientific and Industrial Research, Wellington.

(Received for publication, 18 February 1958)

Summary

Experimental investigations were made in 1954 and 1955 to determine the nature of marine fouling at the Port of Lyttelton. Seasons of settlement and rates of growth are outlined for the dominant marine organisms concerned. These include, Diatoms: *Navicula grevillei* (Ag.) Cleve, Hydroids: *Phialella quadrata* Forbes, *Plumularia setacea* Ellis, Polyzoa: *Cryptosula pallasiana* (Moll.), *Bugula* sp. aff. *B. neritina* (Lamouroux), Serpulids: *Pomatoceros terrae novae* Benham, *Hydroides norvegica* Gunnerus, Barnacles: *Elminius modestus* Darwin, Ascidians: *Asterocarpa cerea* (Sluiter), *Corella eumyota* Traus., *Botryllus schlosseri* (Pallas), *Diplosoma macdonaldi* (Herdman). The sparse settlement on surfaces characteristic of winter months is in great contrast to the heavy fouling occurring in summer when relatively high sea temperatures contribute to accelerated rates of growth in the attached species. In general, settlement is more intense on the south side of the port than on the northern boundary near the main wharves. Observations suggest that dense *Bugula* populations arising on surfaces in summer may be effective in suppressing additional settlement by other species at this time of year. The barnacle, *Elminius modestus,* shows a preference for settlement on long-immersed surfaces, particularly those bearing earlier-established *Elminius* populations, and peak intensities of settlement in autumn and spring may be related to seasonal abundances of food for the planktonic larvae.

INTRODUCTION

A necessary basis for the interpretation of the problem of marine ship-fouling is a knowledge of the varieties, seasonal cycles in reproduction, and growth of those sessile marine organisms to whose settling stages the hulls of vessels in port are exposed. Planned to provide such a background, and to gain an appreciation of regional differences in the occurrence of ship-fouling in New Zealand waters, experimental investigations have been undertaken at the major ports. Traditional procedures, involving the temporary immersion of test surfaces within harbour waters, have been used to determine the forms responsible for local fouling and the seasonal variations and sequences in settlement arising among the dominant species.

Due to limitations of the experimental method, not all members of natural populations of sedentary organisms from intertidal and subtidal regions may be recorded on experimental surfaces. An even smaller proportion of those observed eventually attain any importance in fouling the underwater surfaces of ships, yet, as experience has shown ship-fouling species to be generally well reprsented in the experimental series, the methods fulfil most of the requirements of a general survey.

It is intended to evaluate the status in active ship-fouling of each experimentally observed species in a later communication. The present report describes the annual fouling record of all species concerned in the series of experimental investigations made at the Port of Lyttelton.

LOCALITY

Lyttelton Harbour (Fig. 1) lies on the north-western side of Banks Peninsula, South Island. From the entrance, the harbour extends 8 miles west-south-west at about 1 mile in width. Depths decrease from 16·5m at the entrance to the shallow mud flats at the upper limits. The Port of Lyttelton, some 103 acres in extent, is formed by two breakwaters and lies on the northern side of the Harbour, about 4 miles within the entrance.

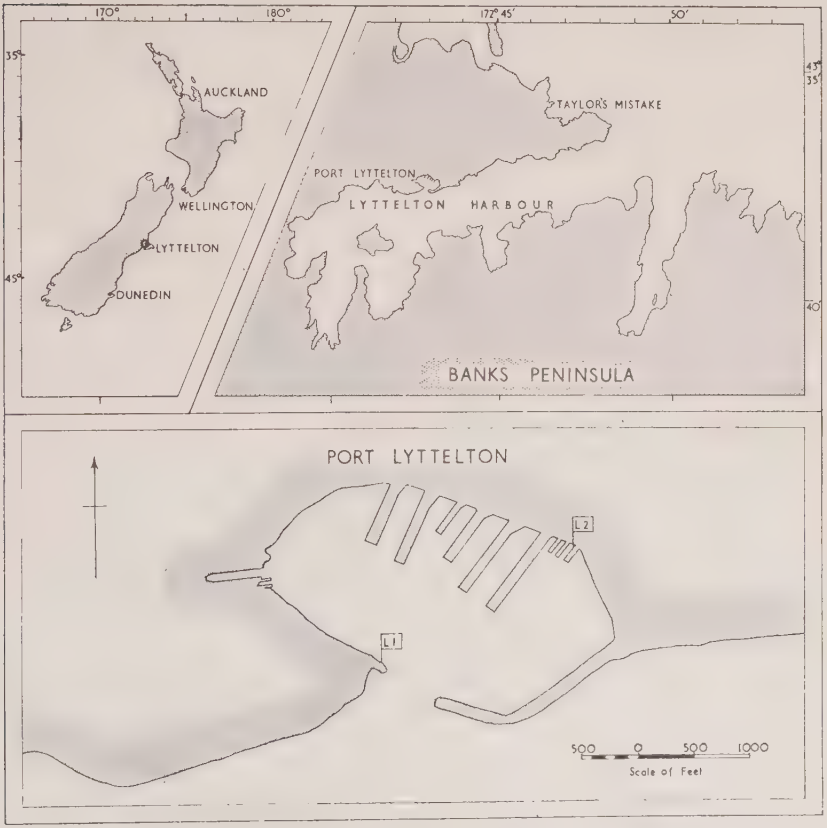

FIG. 1.—Port of Lyttelton, South Island, New Zealand. Locality map showing sites of experimental stations.

Principal port of the Canterbury Province, Lyttelton ranks third port of New Zealand as regards aggregate tonnage of shipping entered. In 1954, the total inwards traffic, both overseas and coastal, was 2,526,747 net tons, or 19% of the total for all New Zealand ports.

The depth of water within the port varies from 12 ft to 38 ft, and tidal ranges are 7 ft at springs, 5 ft at neaps. North-easterlies and south-westerlies are the prevailing winds, the area being most exposed to easterly winds which, however, are of infrequent occurrence.

Sea-water surface temperature records for the Port have been reported previously by Skerman (1958) for the years 1953-55 when experiments were in progress. Temperatures tend to be higher in summer and lower in winter than those of surface waters beyond the harbour entrance, contributing to the relatively wide annual range of some 14° C between extreme values with maxima occurring in January and minima in July.

While a number of marine biological collections have been made within the precincts of the harbour, and systematic studies of various sedentary groups reported, little information is available on their periods of settlement and characteristics of growth. An ecological study (which includes a description of climatic and tidal data for the region) of intertidal rocky-shore communities at Taylor's Mistake (1 mile west of the harbour entrance) has been made by Knox (1953).

METHODS

Apparatus

Surfaces chosen for the collection of fouling were black perspex panels, 6 in. x 6 in. and $\frac{3}{16}$ in. in thickness. Initial trials with plate glass (ground surfaces), asbestos-cement sheets, and perspex, favoured perspex in strength, weight, and comparative efficiency as regards the numbers of organisms attaching. Before use, all panels were rubbed with No. 1 glass paper to produce randomly abraded surfaces.

A rectangular frame, 3 ft long, 7 in. wide, and 7 in. deep, of $\frac{3}{8}$ in. brass rods and $\frac{1}{8}$ in. cross braces was designed to hold 6 removable panels within supporting channels welded to the frame, the panels being secured over their upper edges by split-pins (Fig. 2).

With its long axis horizontal the frame was slung endwise on two phosphor-bronze wires tied to wharf superstructures so that the whole frame was immersed in the water at a depth of 1 ft below E.L.W.S. A brass chain was attached to the mid-point of the frame to facilitate its withdrawal to the surface so that an exchange of panels could quickly be made.

Sites and Orientation

Two frames, designated Stations L1 and L2, were installed in the port as indicated in Fig. 1, L1 at the Oil Wharf and L2 by the Tug

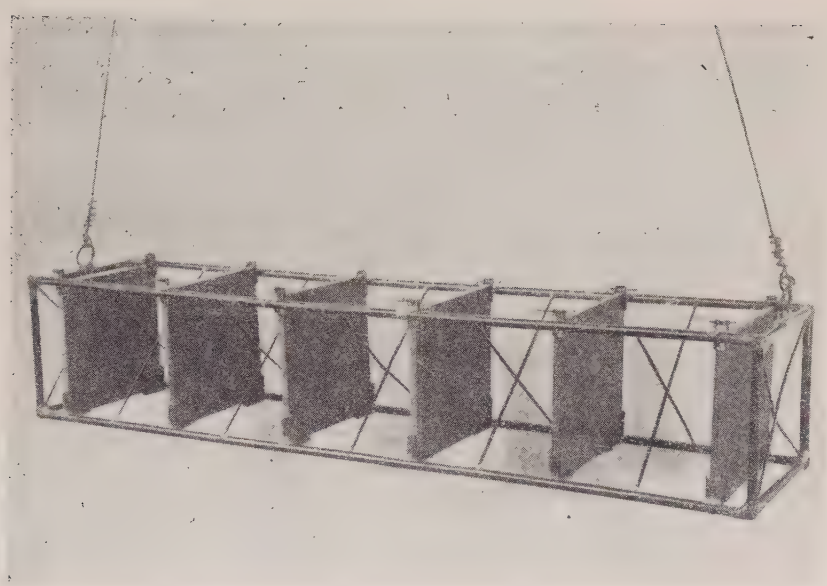

FIG. 2.—Frame containing experimental panels.

Wharf. Frames were placed so that the panel surfaces faced north and south.

Immersion Schedule

To examine the fouling developed on surfaces throughout the year, panels were immersed for varying periods of time, after which they were replaced by clean ones. A schedule was drawn up for the withdrawal and replacement of panels so that one of the six panels in each frame was changed monthly, the second 2-monthly, the third 4-monthly, the fourth 6-monthly, and the fifth 12-monthly. The sixth panel was left in place for the duration of the investigations. Under this scheme, monthly panels provided information on settlement during each month of the year, while those of longer immersion periods showed features of development, longevity, and growth in species contributing to fouling assemblages of increasing ages. Four- and six-monthly panels also showed differences between fouling populations developed from one season to another, in particular, differences in type and abundance of the integral species.

Despatch and Examination of Panels

Immediately after their withdrawal from the frames, fouled panels were placed in a non-corrodible metal container which was then filled to capacity with a 10% neutral solution of formalin in sea-water. The

container was sealed and forwarded to the Wellington laboratory, where panels were photographed and examined as soon as possible after arrival.

In recording the numbers and sizes of organisms present, the central square decimetre of each surface was examined under a travelling binocular microscope, a wire grid delineating 100 square centimetres being placed over the panel to facilitate counting the more abundant varieties. Measurement was made either by ocular micrometer or directly by calipers. Note was taken of the differences in fouling between the side of the panel which had been facing north and the opposite south side.

Duration of Investigations

After preliminary trials of different types of test panels, siting of the stations and arrangements for the withdrawal and despatch of panels in September-November 1953, continuous investigations were begun in March 1954. In February 1955 the frame and panels at L2 were damaged by vandalism and this station was not replaced. Immersion of panels at L1 terminated in November 1955, when it was considered that sufficient data for the purposes of the survey had been accumulated.

SPECIES LIST

All species associated with test-panels of the Lyttelton investigations are listed below.

ALGAE

Diatomaceae

Navicula grevillei (Ag.) Cleve

Chlorophyceae

Cutleria multifida Grev.

Enteromorpha sp.

PORIFERA

Sycon ornatum Kirk

? Halichondria sp.

COELENTERATA

Hydrozoa

Phialella quadrata Forbes

Plumularia setacea Ellis

Actiniaria

? Diadumene neozelanica Carlgren

Madreporaria

? *Flabellum* sp.

POLYZOA

Cryptosula pallasiana (Moll.)
Bugula sp. aff. *B. neritina* (Lamouroux)
Bugula sp. nov. cf. *B. flabellata* (Thompson)
Menipea sp. ? *M. patagonica* (Busk)
Escharoides angela (Hutton)
Tubulipora sp.
Caberea zelandica (Gray)

POLYCHAETA

Serpulidae

Pomatoceros terrae novae Benham
Hydroides norvegica Gunnerus
Spirorbis sp.

CRUSTACEA

Cirripedia

Elminius modestus Darwin
Balanus decorus Darwin

MOLLUSCA

Pelecypoda

Ostrea sinuata Lam.

TUNICATA

Ascidiacea

Corella eumyota Traus.
Asterocarpa cerea (Sluiter)
Molgula mortenseni (Mich.)
Botryllus schlosseri (Pallas)
Diplosoma macdonaldi (Herdman)

MONTHLY SETTLEMENT

From the evidence of panels immersed for monthly periods a month-by-month synopsis of the trends in settlement throughout the year is given as follows.

JANUARY *1955 (L1)*

Greatest intensity of settlement with highest rates of growth took place during this month. Sharing dominance were numerous individuals of the simple ascidian, *Corella eumyota,* and many colonies of the polyzoan *Bugula* sp., growth of the two completely obscuring the panel surfaces. A few

individuals of a second simple ascidian, *Asterocarpa cerea,* were present as well as the colonial form, *Botryllus schlosseri.* The rapidly growing hydroid, *Plumularia setacea,* was common with heights of stems up to 3·5cm. Colonies of the erect polyzoan *Bugula* sp. nov. were interspersed among those of *Bugula* sp. but were many fewer in number. Heaviest growth of all these forms was on the south face of panels, the opposite face bearing numerous tufts of *Navicula grevillei.*

FEBRUARY *1955 (L1)*

Further dense settlements of *Bugula* sp. and *Corella eumyota* continued. Many colonies of *Botryllus schlosseri* established, and attached to areas relatively clear of other growth were a number of serpulids, *Hydroides norvegica.*

MARCH *1955 (L1)*

With diminished intensity of settlement and size, *Bugula* sp. and *Corella eumyota* were again the most abundant colonizers. Further settlements and rapid growth of *Hydroides norvegica* were accompanied by the appearance of a second serpulid, *Pomatoceros terrae novae.* A heavy settlement of *Elminius modestus* occurred and a number of encrusting colonies of *Cryptosula pallasiana* appeared.

APRIL *1954 (L1)*

Corella eumyota and *Elminius modestus* were the most abundant species on generally lightly settled surfaces. Odd *Pomatoceros* tubes were present together with a few minute colonies of *Bugula sp.*
(L2) As at L1, but with a dense settlement of *Elminius modestus.*

MAY *1954 (L1)*

In decreasing numbers the same forms as in April continued settlement. *Corella eumyota* was again dominant but only a small colonization by *Elminius modestus* occurred. A few small colonies of *Bugula* sp .were present.
(L2) As at L1, but with fewer *Corella* and *Elminius.*
1955 (L1)
Similar settlement to that of 1954, with the additional appearance of fine filaments of *Enteromorpha* sp., particularly on the northern faces of panels.

JUNE *1954 (L1)*

A conspicuous diatom primary film covered surfaces which bore very sparse macroscopic growth. Small *Corella* individuals were the most abundant, followed by a few *Elminius.*
(L2) As at L1, but bearing a heavier settlement of small *Corella.*
1955 (L1)
Similar to L1 of 1954, but with a lighter diatom film.

JULY *1954 (L1)*

Coinciding with a period of prevailingly low sea temperatures, settlement on surfaces was least of all months observed. A light diatom film was present with several patches of aggregated stalked protozoa (*Vorticella* sp.). Macroscopic forms were limited to a few *Corella.*
(L2) Rather more *Corella* and a heavier diatom film, otherwise similar to L1.
1955 (L1)
Similar to L2 in 1954, with more widely distributed colonial protozoa.

AUGUST *1955 (L1)*

In marked contrast to the sparse settlement in July, panels withdrawn at the end of August bore an appreciable amount of growth, in which algae predominated. The many small tufts of the ensheathed diatom *Navicula grevillei,* and numerous filaments of *Enteromorpha* sp., particularly on the northern faces of panels, were widely distributed. Much particulate sediment, enmeshed by these forms, covered the panel surfaces. A few *Elminius modestus* settled.

SEPTEMBER *1953 (L1)*

Generally light settlement in which algal fouling by *Navicula* and *Enteromorpha* sp. predominated.

(L2) As L1.

1954 (L1)

Both alagal forms, *Navicula* and *Enteromorpha,* were dominant and a few scattered *Corella* were present.

(L2) The two algal forms were similarly dominant, but many more *Corella* appeared than at L1. Small *Elminius modestus* were noted at L2.

1955 (L1)

A heavy settlement of *Elminius modestus* dominated the south face, while algal fouling was more abundant on the opposite side.

OCTOBER *1953 (L1)*

In contrast to the predominant algal fouling on August and September panels was the appearance of extensive animal fouling on surfaces withdrawn at the end of October. These bore heavy settlements of the hydroid, *Phialella quadrata.* Of secondary importance were a number of *Elminius modestus* and tufts of *Navicula.* A few *Corella* were present.

(L2) With the addition of a few colonies of *Botryllus schlosseri,* similar to L1.

1954 (L1)

Phialella quadrata was dominant and evenly distributed over all surfaces. Numerous *Corella* and tufts of *Navicula* were present. Several colonies of *Botryllus schlosseri* established together with a second colonial form, *Diplosoma macdonaldi.* There was a light settlement of *Elminius modestus.* (L2) Settlement was much lighter than at L1. *Phialella quadrata* dominated surfaces with lighter settlements of *Corella eumyota* and *Elminius modestus.*

NOVEMBER *1953 (L1)*

As in October, surfaces were again dominated by densely settled *Phialella quadrata,* colonies of which were larger in size than in the previous month. Light settlements also occurred of *Corella eumyota, Botryllus schlosseri,* and *Elminius.*

(L2) Surfaces differed from those at L1 by bearing a heavy growth of *Navicula.* The hydroid *Phialella quadrata* was also abundantly represented with *Corella* and *Elminius,* there being more numerous individuals of the latter than at L1.

1954 (L1)

Generally heavier settlement than in 1953 took place with *Phialella quadrata* as the dominant species, followed by many *Corella* and *Botryllus.* Numerous *Enteromorpha* filaments developed on the north-facing surface. A second hydroid, *Plumularia setacea* was abundant on south faces and light settlements took place of the two serpulids, *Pomatoceros terrae novae* and *Spirorbis* sp. Several small colonies of *Bugula* sp. nov. developed.

(L2) Settlement was appreciably lighter than at L1, with *Phialella* and *Corella* evenly distributed, and a light settlement of *Elminius*.

DECEMBER *1954 (L1)*

Heavy colonization of surfaces occurred with *Phialella quadrata, Corella eumyota,* and *Bugula* sp. sharing dominance. Spreading *Botryllus* colonies were conspicuous, together with those of *Diplosoma macdonaldi*. Long stems of the hydroid *Plumularia setacea* were commonly distributed over surfaces as well as colonies of the erect branching polyzoan *Menipea* sp. No *Elminius* barnacles settled.

(L2) The lighter settlement than at L1 was dominated by *Corella* and *Botryllus* and to a lesser extent, *Phialella*. Numerous minute colonies of *Bugula* sp. were present with a few small serpulids, *Pomatoceros terrae novae*, and *Spirorbis* sp.

A summary of the annual record of settlement is given in Fig. 3. This outlines periods of settlement for the more important species and the months of their maximum intensity of settlement. Data has been taken from the observations from April 1954, until March 1955, and the sequence rearranged to conform with a graphical method adopted by the Woods Hole Oceanographic Institution (1952) for representing characteristics of marine fouling in various ports of the world.

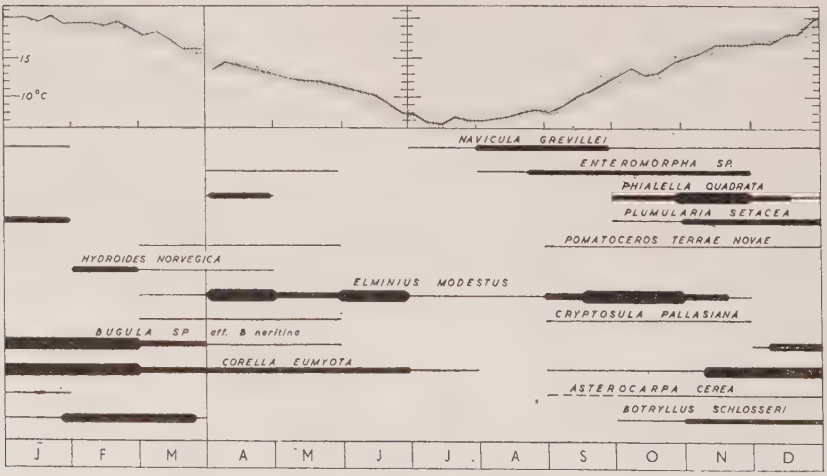

FIG. 3.—The annual record of settlement of fouling organisms at Lyttelton. Mean temperature, solid line; range between extreme temperatures, shaded.

THE FOULING SPECIES

ALGAE

Navicula grevillei (Ag.) Cleve

Greenish tufts, consisting of thread-like mass of this ensheathed diatom were conspicuous features of panels from July-August to

November and from January to April. Attachment was usually confined to one surface of each panel only—that facing north and more exposed to direct sunlight. In the winter and early spring months, when settlement of other organisms was particularly low, this form dominated. Dense establishments were accompanied by the accumulation of much sediment on the panel surface about the bases of the diatom clumps.

GROWTH. Measurements made in terms of overall average height of clumps are indicated below in comparison with the duration of immersion of the surfaces from which they were taken.

TABLE 1.—Seasonal Growth in *Navicula grevillei*.

IMMERSION (months)	PERIOD	MEAN HEIGHT (cm)
1	April	0·4
1	September	0·5
1	October	0·5
1	November	1·0
1	January	1·0
2	May-June	3·0
2	July-August	1·0
2	September-October	3·5
4	June-September	4·0
4	June-September	5·0

Enteromorpha sp.

Monthly panels of August, September, and November bore minute filaments of *Enteromorpha* in considerable density. This alga was not recorded in any abundance on longer immersed surfaces, neither did its filaments grow beyond a few millimetres; presumably the conditions of permanent submergence at the depth panels were set were inappropriate for normal survival and growth. It may be added that locally-based fishing and pleasure craft, as well as the inter-Island passenger ferries which berth at Lyttelton by day, all suffer intense *Enteromorpha* fouling at water-line regions during the early spring months. Probably, this period represents the main phase of settlement of this organism, while a lighter autumn period of settlement occurs from April to May.

Cutleria multifida Grev.

Samples of this species were taken from two panels withdrawn in November. 1954, after six months immersion. Overall lengths of specimens were 2·0 to 2·5 cm, and, as this form was not observed on any short-term panels, the time of settlement is unknown.

Porifera

Sycon ornatum Kirk

The briefest immersed surface on which this calcareous sponge occurred was a 2-month panel withdrawn in April 1954, which bore individuals averaging 1·5 cm in height. Other panels, immersed for varyingly longer periods, and bearing specimens of this size, were some withdrawn in November of 1954 and 1955. These data indicate that the individuals observed developed from larval settlements taking place in March-April and in October-November. The apparent absence from monthly panels may be attributed either to a failure to attain recognizable size in one month, as was suggested by Ralph and Hurley (1952) in their Wellington investigations, or to an inability of larvae to attach successfully to clean, new surfaces.

On several long-term immersions during 1954, sizes of individuals averaged 2·0 cm in height from panels withdrawn in May, 3·0 cm from panels withdrawn in July, and 3·5 to 4·0 cm from panels withdrawn in September. This sequence of sizes suggests that all these individuals may have initially settled during the previous March-April period.

? *Halichondria* sp.

This species was present on a panel that had been immersed 20 months. It was also attached to rods of the brass frame at L1 and several large colonies were spreading over clumps of the simple ascidian *Molgula mortenseni*. While the time of its initial settlement is unknown, the above evidence indicates that by virtue of its capacity for expansive growth, this species may occupy an important position in long-established fouling communities.

Hydroids

Phialella quadrata (Forbes)

This was the most important organism fouling surfaces during the spring and early summer, and its appearance in October marked the onset of the heavier fouling associated with warmer months of the year. Settlement continued until December, with peak intensity in November, when dense masses of growth of up to 20 individual colonies per square centimetre developed. Densest settlement took place on the clean surfaces of recently set panels, and on those which had been initially set down during the winter, and by October bore relatively little other growth. Lighter epizoic colonization occurred on longer immersed panels carrying appreciable quantities of growth originally attaching during months preceding the winter. In addition to the main settling period, light settlements were recorded at both stations in April 1954, and again at L1, the only station operating in this month of 1955.

The colonization of panels by *Phialella* was consistently more abundant at L1 than at L2, a trend illustrated in Fig. 4 which also indicates the mean maximum height reached by colonies at the end of each month of settlement as recorded at both stations in 1954. The largest specimens of this species observed during the investigations had stems averaging 2·0 cm in height. If this represents the maximum size, it appears that such is attained in a little over a month's growth during the November-December period.

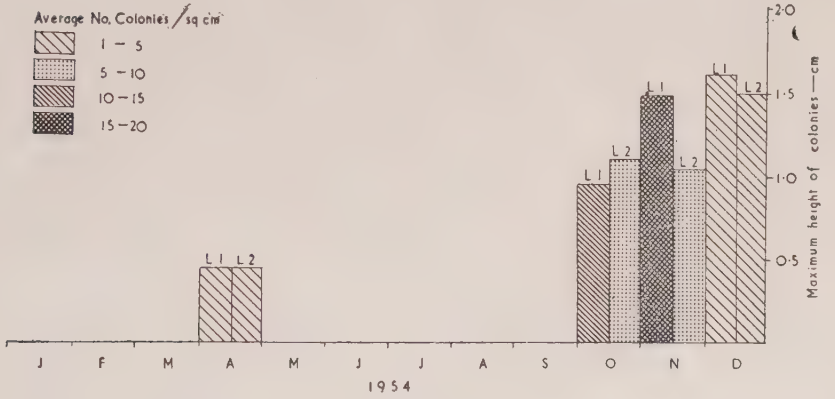

FIG 4.—Density of settlement and growth in *Phialella quadrata*.

Plumularia setacea Ellis

This species, which settled from October to January, was never abundantly represented on test panels. Its most conspicuous feature was its rate of growth, stems of colonies measuring 2·5 cm in height at the end of both October and November, and 3·0 to 3·5 cm in December and January, all after one month's immersion. On 2-monthly panels, colonies averaged 4·0 cm in height (November to December) and on a panel immersed for 3 months (October to December), 6·0 cm.

ACTINIARIA

? *Diadumene neozelanica* Carlgren

Two specimens only were found on a panel that had been immersed 20 months at L1. Basal diameters were 2·0 cm and 3·5 cm respectively, and both individuals appeared to have been established for a considerable time.

MADREPORARIA

? Flabellum sp.

The single monthly record of small solitary corals developing during October 1953, is probably an inadequate representation of settlement characteristics for the species. Six further specimens of similar size (0·5 cm in overall height) were taken from a panel immersed in June 1954, and withdrawn the following November. Other records included an extensive establishment of coral-colonies (1·0 to 2·0 cm height) on a 9-month panel immeresd from August 1953 to May 1954. Comparison of these sizes suggests that settlement took place in the spring and early summer.

POLYZOA

Cryptosula pallasiana (Moll.)

Although the most common of encrusting polyzoan colonies recorded, this species was not a prominent member of young fouling assemblages. Panels immersed six or more months, however, bore large colonies of *C. pallasiana* some 12 sq cm in area over free panel surfaces, and it appeared that through its ability to spread over a large surface area, this species might occupy prominent position in aged fouling communities. Settlement was mainly confined to September, October, and November, but a lighter autumn settlement was evident during March, April, and possibly May. Exclusion effects, to be discussed later in the cases of other species, might have prevented summer settlement of *Cryptosula*, a slow growing, basally attaching form which may have suffered in competition for free surface with the abundantly-settling ascidians and erect, branching *Bugula* species.

Sizes of colonies up to 1 month since settlement averaged 0·5 sq cm in area for the months of September, October, and November, and larger colonies of 1·5 sq cm developed in March of 1955. Colonies established in the September-November period of 1954 occupied areas of 12 sq cm by the following May, while autumn-settling colonies in 1954 were only 2·0 sq cm in size at the onset of the subsequent spring settling period in September.

Bugula sp. aff. *B. neritina* (Lamouroux)

The commonest branching polyzoan encountered at Lyttelton, this species attached to panels during the 1954-55 summer from December to May. Dense settlement, coupled with a high rate of growth contributed to the dominance of this form on all surfaces, both new and previously colonized by other growths, during the mid-summer months. Newly immersed panels collected numerous young *Bugula* colonies in a very short time, particularly during February 1955, while epizoic colonies developed with equal success on panels already fouled by the hydroid *Phialella quadrata* and simple ascidians in December.

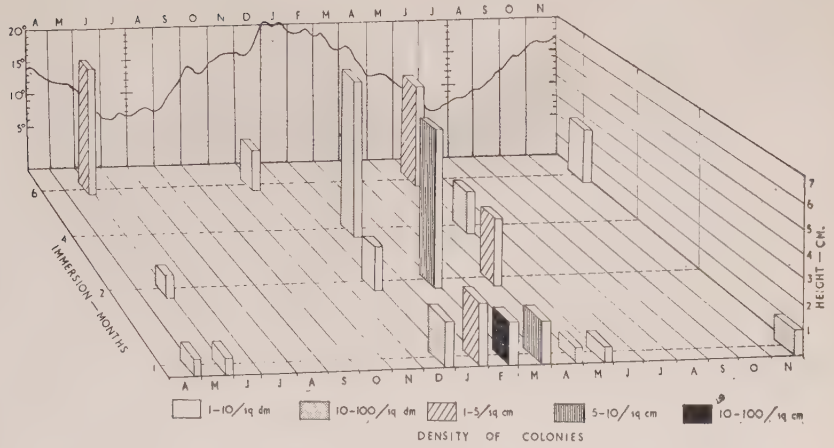

FIG. 5.—Seasons and density of settlement, and growth in *Bugula* sp. aff. *B. neritina*.

Patterns of the settlement, abundance and growth of *Bugula* sp. are shown diagrammatically in Fig. 5. Heights of the pillars are proportional to the height of the largest colonies present and the abundance of colonies is represented by the intensity of shading on the left-hand vertical faces of the pillars. Each pillar is based opposite the month of withdrawal of the panel concerned, and pillars are arranged in rows from front to back according to the immersion periods undergone. To the rear of the diagram sea-surface temperatures have been plotted from the means for 6-day periods in order to show how the characteristics of rapid colony growth in this species were associated with the highest sea temperatures of the year. In interpreting the diagram, it is important to note that the immersion period of any panel does not necessarily represent the real age of the colonies attached to it. For instance, colonies of some 7·0 cm in height borne by the panel withdrawn at the end of January 1954, had not developed over the full immersion period of 4 months, for, as can be seen by reference to the monthly withdrawals in the front rank, larval settlement did not commence until December. Thus, the maximum probable age of these 7·0 cm colonies was two months.

Few of the large growths developed in the summer appeared to persist throughout the remainder of the year. Panels immersed 11 and 20 months bore colonies whose sizes point to original settlement as having taken place during the immediately preceding summer, not earlier. There were a number of indications from long-term panels that the large colonies of *Bugula* sp. developed during the summer, eventually stripped from the panels on prolonged immersion, possibly due to an excessive strain imposed on the basal stems and root filaments of

colonies by the establishment and extensive growth of colonial ascidians which covered, and sometimes enveloped them. The dominance of *Bugula* sp. on such surfaces may, therefore, be short-lived and confined to the summer months and for a brief time afterwards.

It is noteworthy that the first post-winter appearance of *Bugula* sp. in 1954 occurred in December, but in 1955 in November. Sea temperatures were on the average a degree C higher during the first fortnight of November 1955 than in November 1954, a possible explanation for the earlier onset of larval settlement in the later year.

Bugula sp. nov. cf. *B. flabellata* (Thompson)

Only one record of this erect polyzoan was obtained from a monthly panel, in November 1954. The species was generally poorly represented on short-term immersions, but in long-developed assemblages, relatively large colonies were commonly found. The season of settlement of this form is indefinite, but inspection of its occurrence on panels immersed 4 and 6 months suggest that attachment took place in the late autumn and early summer.

The species was equally well represented at L1 and at L2. Its persistence on long-immersed surfaces was a contrasting feature to *Bugula* sp. aff. *B. neritina*.

Menipea sp. ? *Menipea patagonica* (Busk)

This species settled on monthly panels in November and December of 1954, and in January and November of 1955. Only a few colonies were present on each occasion, and their maximum height was from 8 to 10 mm.

Escharoides angela (Hutton

One small colony of this species was noted on an 11-month panel withdrawn in July 1954. A second long-term panel, immersed 20 months at L1, bore two 4-sq cm colonies on withdrawal in November 1955.

Tubulipora sp.

A small colony on a 4-month panel withdrawn from L2 in September 1954, constituted the single record of this species.

Caberea zelandica (Gray)

Three colonies, 1·0, 1·5, and 3·0 cm in height were attached to a 6-month panel withdrawn from L1 in November 1955.

SERPULIDAE

Pomatoceros terrae novae Benham

Settlement of this species was noted between September and December, and in March, April, and May. It is possible, however, that successful establishment on panels in the intervening months of January and February may have been precluded by the growth of polyzoans and ascidians on panels during the height of the summer. Observations of

settlement and growth in *Pomatoceros terrae novae* on panels are given in Table 2. Data has been combined from both stations, but serpulids generally were more numerous at L1 than at L2.

TABLE 2.—Seasonal Settlement and Growth in *Pomatoceros terrae novae*.

IMMERSION (months)	PERIOD	NO. INDIVIDUALS (per sq dm)	MEAN OVERALL LENGTH (cm)	PROBABLE MONTH OF SETTLEMENT
1	March	4	0·3	March
1	April	1	0·2	April
1	September	6	0·6	September
1	September	3	0·5	September
1	September	3	0·7	September
1	November	2	0·5	November
1	December	1	0·5	December
2	April-May	4	1·5	April
2	September-October	14	2·0	September
2	September-October	2	1·2	September
3	March-May	4	2·5	March-April
3	September-November	10	2·0	September
3	September-November	1	3·0	September
5	May-September	7	3·0	May

Hydroides norvegica Gunnerus

Settlement of this species was confined to the months of February, March, and April. Individuals differed from those of *Pomatoceros terrae novae* in their greater rates of growth and in the orientation of their calcareous tubes on long-immersed surfaces when these were crowded with other growths. Under these conditions, particularly during February and early March when polyzoan colonization was heavy, tubes grew out in a direction normal to the surface so that apertures projected several centimetres from the level of basal attachment.

Details of settlement and growth in *Hydroides* are included in Table 3.

TABLE 3.—Seasonal Settlement and Growth in *Hydroides norvegica*.

IMMERSION (months)	PERIOD	NO. INDIVIDUALS (per sq dm)	MEAN OVERALL LENGTH (cm)	PROBABLE MONTH OF SETTLEMENT
1	February 1955	21	0·5	February
	March 1955	12	0·5	March
2	March-April 1955	12	2·5	March
3	February-April 1955	10	3·0	February-March
6	December-May 1955	6	2·0	March-April
12	September-September 1955	2	3·0	February-April 1955

Spirorbis sp.

Few tubeworms of this species appeared during the investigations. Records were taken from monthly panels of March, November, and December, but further evidence from 2-monthly panels indicated that settlement also took place in April and October.

CIRRIPEDIA

Elminius modestus Darwin

The presence of this barnacle in widely varying numbers on most monthly panels other than those of December, January, and February, might at first be taken as an indication that this species is capable of settlement throughout the whole year except during the mid-summer. On the other hand, absence from the summer panels could also be ascribed to competitive factors for, like the serpulids, barnacles require a relatively solid, intact surface for successful settlement and such may not have been available in these months when panels were covered by numerous polyzoan colonies. Although no young barnacles were to be found on any panels during January and February, cyprids were occasionally seen enmeshed among branches of polyzoan colonies. The identity of these cyprids was not confirmed and could have belonged to any of the common local species. But, in view of the fact that *E. modestus* was the only form consistently encountered in the investigations, there seems to be a greater probability of the larvae being of *Elminius* stock than of any other. If this were so, the absence of barnacle-setting on panels in summer may not have been due to any prevailing lack of larvae. It is unlikely that the high summer temperatures at Lyttelton during January and February imposed any restrictions on spawning or larval development, for this species settles prolifically during these months in Auckland Harbour, where summer temperatures average 3° to 4° C higher than in Lyttelton.

A notable contrast between certain monthly panels and others of longer immersion but withdrawn at the same time, was the fact that the latter frequently bore many more young barnacles of the same size as were on the monthly panels. The similarities in size suggest corresponding ages, and therefore at the time of settlement, more individuals must have established upon the previously immersed surfaces than on the newly placed ones. In Fig. 6, two panels, *A* and *B*, are shown after their withdrawal in September 1954, *A* having been immersed 1 month, and *B*, 4 months. The numbers of barnacles attached to *B* greatly exceed those on *A*. Barnacles on panel *B* were all of a similar size range to the few on panel *A*, and all are assumed to have settled during the month prior to withdrawal, that is, September. The surface *B* otherwise differed from *A* in carrying a heavier diatom film, much more particulate sediment, a growth of filamentous algae, and a few polyzoan colonies.

A comparison of the numbers of young, similar sized barnacles attached to long- and short-term panels withdrawn simultaneously is given in Table 4.

FIG. 6.—Differing intensities of *Elminius* settlement on two panels after their simultaneous withdrawal, *A* having been immersed 1 month, *B*, 4 months. Barnacles on both panels are all about the same size.

TABLE 4.—Comparison of the Numbers (per sq dm) of *Elminius modestus* Barnacles on Monthly Panels with those of the Same Size Range on Long-Term Panels.

	SHORT TERM		LONG TERM	
PANELS WITHRAWN	IMMERSION PERIOD (months)	NO. BARNACLES	IMMERSION PERIOD (months)	NO. BARNACLES
May 1954 (L1)	1	2	2	4
(L2)	1	3	9	4
May 1955 (L1)	1	1	4	4
Jun. 1954 (L1)	1	6	2	925
Jun. 1955 (L1)	1	2	2	109
Oct. 1953 (L2)	1	26	2	289
Oct. 1954 (L1)	1	26	4	164
(L2)	1	5	4	555
Nov. 1953 (L2)	1	11	3	111
Nov. 1954 (L2)	1	6	6	87

It is evident, then, that the record of monthly panels may give little real indication of barnacle settlement during any month, indeed, as shown above, barnacles may almost fail in attaching to a monthly panel while a dense settlement suceeds on a neighbouring (fouled) surface. In general, the numbers of barnacles attaching to monthly panels were low and variable.

An attempt has been made to outline the intensities of *Elminius* settlement throughout the year by incorporating data from all panels on which barnacles occurred. This has been done by making approximate age estimations of barnacles on the basis of their size—size having been indicated in terms of the measured rostro-carinal diameter. If the maximum size attained by young barnacles at the end of their

TABLE 5.—Maximum Sizes of *Elminius modestus* Barnacles of up to 1 Month in Age. Data has been Taken from Monthly Panels, 1954-55.

MONTH	MEAN SEA TEMPERATURE (° C)	TOTAL NO. BARNACLES	MAXIMUM SIZE (diam. in mm)
January	19·9	No settlement	No settlement
February	19·3	No settlement	No settlement
March	17·2	12	2·6
April	14·0	392	1·9
May	11·9	5	1·0
June	9·0	8	0·8
July	7·2	26	0·7
August	7·7	25	0·6
September	10·2	6	0·9
October	12·4	50	1·8
November	15·7	31	2·4
December	17·3	No settlement	No settlement

first month of settlement were known, then it would be possible to estimate approximately how many of the total number of individuals borne by any panel had settled during the period of up to a month preceding withdrawal of the panel. For these purposes, maximum sizes for month-old barnacles have been taken from the records of the monthly immersion series. It has been necessary to include data from each calendar month in view of the seasonally varying rates of growth. These details are set out in Table 5.

These maximum sizes have been used to assess the minimum probable number of barnacles settling during the last month of immersion of any panel by counting the numbers falling within the maximum size groups appropriate to the month of withdrawal. Probable numbers of barnacles, estimated by this method, which settled on long-term panels during their last month of immersion are set out in Fig. 7. As the largest barnacles on monthly panels may not have been necessarily 1 month old, the observed maximum sizes of Table 5 may fall short of the real maxima for 1 month's growth. This would result in an under-estimation of probable numbers in Fig. 7. Furthermore, the monthly maximum size ranges given in Table 5 do not take into account individual variations in rates of growth in any one month. While the actual numbers of barnacles deduced are therefore of approximate value only, it is apparent that pronounced cycles in the intensity of settlement took place in the years concerned, with periods of densest colonization occurring during the autumn and spring months. The significance of these periods of peak settlement by *Elminius modestus* will be discussed later.

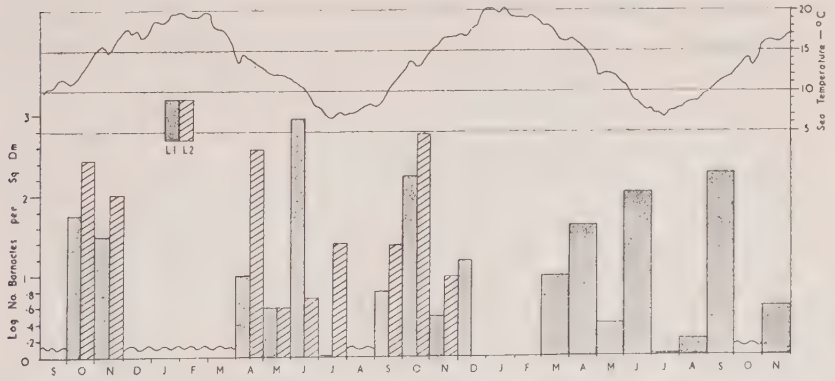

FIG. 7.—Estimated monthly settlement of *Elminius modestus* barnacles on long-term panels. Wavy line = no record.

A second point illustrated in Fig. 7 is the tendency for barnacle settlement to be more dense at L2 than at L1.

GROWTH. In this investigation it was not practicable to follow the rates of growth of marked individual barnacles on permanently submerged surfaces. Some appreciation of trends in growth under the

conditions of the test series can be gained from comparison of the sizes of barnacles after different immersion periods. All measured barnacles from the central square decimetre of each panel were counted in 0·5 mm size groups. Numbers, and the largest size groups associated with panels immersed 2 or more months are given in Table 6.

TABLE 6.—Largest Size Groups Attained by *E. modestus* Barnacles Upon Panels Immersed for Varying Intervals of Time During Different Periods of the Year.

Immersion (months)	Period	Range of Monthly Mean Temp. (° C)	Total No. Barnacles	Max. Size Range (mm)	No. Barnacles Within Max. Range
2 (L1)	Apr.-May 1954	14·0-11·9	6	1·6-2·0	1
(L1)	May-Jun. 1954	11·9- 9·8	962	0·6-1·0	955
(L2)	Aug.-Sept. 1954	7·7-10·0	93	1·6-2·0	4
(L1)	Sept.-Oct. 1954	10·2-12·4	63	1·6-2·0	3
(L2)	Sept.-Oct. 1954	10·2-12·4	291	2·1-2·5	21
(L1)	Nov.-Dec. 1954	16·2-17·9	24	3·1-3·5	2
(L2)	Nov.-Dec. 1954	16·2-17·9	2	2·5-3·0	2
(L1)	May-Jun. 1955	11·9- 9·0	115	0·6-1·0	114
(L1)	Jul.-Aug. 1955	7·4- 8·6	5	0·6-1·0	5
3 (L1)	Sept.-Nov. 1953	10·2-15·7	117	3·6-4·0	2
(L2)	Sept.-Nov. 1953	10·2-15·7	117	5·1-5·5	4
(L1)	Feb.-Apr. 1955	19·3-15·2	81	4·1-4·5	2
4 (L1)	Jun.-Sept. 1954	7·2-10·0	15	2·1-2·5	2
(L2)	Jun.-Sept. 1954	7·2-10·0	836	2·1-2·5	5
(L1)	Jul.-Oct. 1954	7·2-13·4	229	6·1-6·5	7
(L2)	Jul.-Oct. 1954	7·2-13·4	589	4·1-4·5	2
(L1)	Oct.-Jan. 1955	13·4-19·9	6	4·1-4·5	2
(L1)	Jan.-Apr. 1955	19·3-15·2	122	5·1-5·5	2
(L1)	Jun.-Sept. 1955	7·4-10·1	200	1·6-2·0	45
6 (L1)	Jun.-Nov. 1954	7·2-16·2	11	5·1-5·5	3
(L2)	Jun.-Nov. 1954	7·2-16·2	231	5·6-6·0	7
(L1)	Dec.-May 1955	19·9-11·9	14	3·6-4·0	3
(L1)	Jun.-Nov. 1955	7·4-16·3	11	6·0-6·5	2
9 (L2)	Sept.-May 1954	10·2-19·5	38	5·6-6·0	1

Although, with the information available, it has not been possible to give consideration to individual variations in growth rate, which may be even greater than the size intervals arbitrarily selected, some general points are evident from these data. Comparison of figures for identical immersion histories from both L1 and L2 shows the tendency, previously mentioned, for greater numbers of barnacles to have established at the latter site. Similarly, larger sizes appear to have been attained by barnacles at L2, possibly because the more extensive settling there took place on panels sooner after immersion than at L1. Seasonal temperature influences upon growth rate, previously demonstrated for monthly panels, are also apparent from the data of the 2-monthly series.

Some indication of the possibility of a second seasonal influence on *Elminius* settlement and growth is seen in the group of 4-monthly immersions. If the growth rate is influenced by prevailing sea temperatures as has been suggested by the above data, it might be expected that the largest barnacles in this series would have developed on the panel immersed from October 1954 to January 1955. From other evidence, abundant spring settlement in September-November 1954, took place and in all probability, this would have been represented on the 4-month panel during its first two months of immersion. Only 6 individuals were, however, present on withdrawal in January, and the largest size of these was well below the 4-month maximum for *Elminius* in the investigations. Similarly, the panel immersed 9 months from September 1953 ,to May 1954 (Table 6, bottom line) bore surprisingly few barnacles, only one of which was of a large size. As will be discussed later, these apparent discrepancies in summer settlement and growth might be attributed to the effect of the prolific settlements of the polyzoan, *Bugula* sp., which may have competitively depleted the spring-settling barnacle population on panels and retarted the growth rate of the survivors.

Balanus decorus Darwin

The presence of 5 individuals, some 5 mm in rostro-carinal diameter, on a 2-monthly (September-October) panel in 1954 contributes little information on the seasonal incidence of this species. One further record of a single specimen 8 mm in diameter, from a 6-monthly panel withdrawn at the end of the following month (November) indicates that all these individuals probably settled during October.

MOLLUSCA

Ostrea sinuata Lam.

Only four individuals were found on panels. Three, taken from a panel withdrawn in September 1954, after 9 months' immersion, measured 1·6, 0·6, and 0·7 cm (umbo to ventral margin). The fourth, 1·8 cm, was taken from a 6-month panel withdrawn in May 1955, and it is therefore uncertain when these may have settled.

ASCIDIANS

Corella eumyota Traus.

By virtue of its capacity for settlement throughout almost the entire year, *C. eumyota* became the most important single species associated with all surfaces immersed up to 4 months. Individuals were noted on all monthly panels except those of August in both 1954 and 1955. Periods of most intense settlement were from November to February, but in the winter months of June and July up to 20 individuals per square decimetre were found on panels almost devoid of other macroscopic growth.

An outstanding feature of the *Corella* records was the variation in apparent rates of growth of attached individuals during different months of the year. Assuming that the size of the largest specimens, after a maximum of one month since settlement, is directly related to the rate of growth during this period, the plot of maximum sizes month by month is shown to follow closely the trends in sea-surface temperature, largest monthly sizes being attained in January, least in June-September. Patterns of seasonal growth are reproduced in a diagram (Fig. 8) in which maximum sizes of individuals are represented in the vertical height of wedges which are set out in ranks according to the duration of immersion of the respective panels. The bases of the wedges overlie the periods during which the panels were in the water. Size is expressed as the greatest overall length of the specimens. As all material was in the preserved state by the time measurement was made, the ascidian bodies would have been retracted, thus the lengths given cannot be considered real, the discrepancy between live, extended individuals, and those preserved being greatest in the cases of the larger specimens. For comparative purposes, however, the relative picture of seasonally varying trends in growth rate is unlikely to be much affected.

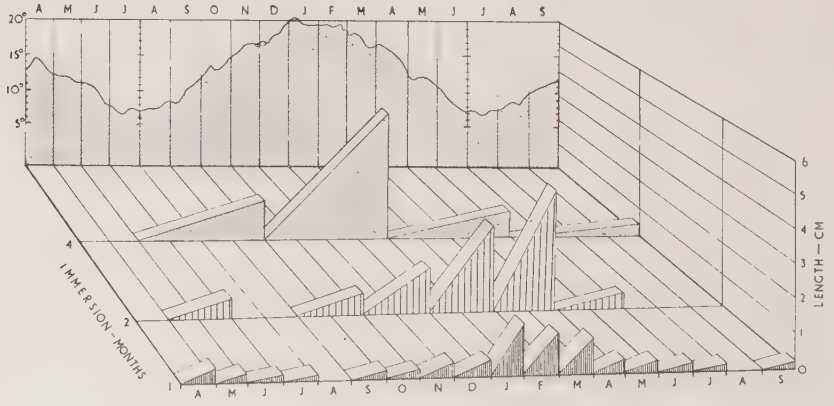

FIG. 8.—Seasonal growth in *Corella eumyota*.

Corella eumyota, with the polyzoan *Bugula* sp., was of pre-eminent importance in the summer fouling of panels immersed from one to two months, but it was noted that this species, despite its prolific colonization of new surfaces, did not appear to survive within aged, complex fouling assemblages.

Asterocarpa cerea (Sluiter)

In comparison with *Corella eumyota,* this form had a much more restricted period of settlement to the spring and early summer months and only few individuals were recognized on monthly panels during this time. Yet on panels immersed four and six months between September and February, *Asterocarpa* was the outstandingly dominant ascidian, and it appears that this species replaced or excluded *Corella* on the prolonged immersion of surfaces to which both species had initially attached with *Corella* in numerical superiority. Previous observations of the replacement of *Corella* by *Asterocarpa* on long-term surfaces have been made by Ralph and Hurley (1952).

Due to its comparative rarity on monthly panels, the settling times for *Asterocarpa* have been inferred from its occurrence on longer-immersed panels. The full record of the species is set out in Table 7.

TABLE 7.—Seasonal Settlement and Growth in *Asterocarpa cerea.*

IMMERSION (months)	PANEL WITHDRAWN	NO. INDIVIDUALS (per sq dm)	MEAN LENGTH (cm)	PROBABLE TIME OF SETTLEMENT
1 (L1)	November 1954	6	0·5	November
(L2)	November 1954	5	0·5	November
2 (L1)	December 1954	50	2·5	Nov.-Dec.
(L2)	December 1954	20	1·5	Nov.-Dec.
(L1)	February 1955	11	4·0	January
4 (L2)	September 1954	2	0·5	September
(L1)	January 1955	35	3·0	Oct.-Dec.
6 (L1)	November 1954	67	2·0	Sept.-Nov.
9 (L1)	September 1955	8	4·0	Summer 1954

Molgula mortenseni (Mich.)

This solitary ascidian appeared on three panels only as detailed below.

The times of settlement on these data are therefore uncertain, but probably autumn and spring.

TABLE 8.—Settlement of *Molgula mortenseni*.

IMMERSION (months)	PANEL WITHDRAWN	No. INDIVIDUALS (per sq dm)	LENGTH (cm)
3	April 1955	5	0·8
4	September 1954	8	0·4
9	May 1954	30	1·0-2·0

Botryllus schlosseri (Pallas)

With an equal ability to establish itself on the clean surfaces of recently set panels as upon previously settled fouling growths, this compound ascidian was a familiar form on many panels in the experimental series. The occurrence of *Botryllus* on surfaces after varying immersion periods is given below. The sizes of colonies was estimated as total area in sq cm occupied by tests of individual colonies.

TABLE 9.—Seasonal Settlement and Growth of *Botryllus schlosseri*.

IMMERSION (months)		PANEL WITHDRAWN	No. SEPARATE COLONIES (per sq dm)	AVERAGE SIZE (sq cm)
1	(L1)	November 1953	4	2·0
	(L2)	April 1954	1	1·0
	(L1)	October 1954	7	1·0
	(L1)	November 1954	32	1·0
	(L2)	November 1954	4	0·5
	(L1)	December 1954	6	2·0
	(L2)	December 1954	13	1·0
	(L1)	February 1955	12	2·5
	(L1)	March 1955	19	1·5
2	(L1)	May 1954	1	1·0
	(L2)	June 1954	1	1·0
	(L1)	October 1954	1	0·5
	(L2)	December 1954	7	6·0
	(L1)	February 1955	3	6·0
	(L1)	April 1955	10	5·0
3	(L1)	November 1953	6	8·0
	(L2)	November 1953	9	6·0
4	(L1)	September 1954	11	2·5
	(L1)	January 1955	4	1·0
	(L1)	April 1955	14	3·0
	(L1)	September 1955	2	2·5
6	(L1)	November 1954	5	1·0
	(L1)	May 1955	(numerous coalescing)	25·0 (total)
	(L1)	November 1955	20	2·0

Although settlement on monthly panels occurred from October to April, it is apparent that colonies also established during September, and in May and June from the presence of small individual colonies on longer immersed panels. Peak intensities of settlement occurred from November to March, during which time the tests of *Botryllus* colonies were to be found on surfaces of panels overlying the simple ascidians, *Corella* and *Asterocarpa,* and spreading over branches of polyzoan colonies. The species was observed as commonly at L1 as at L2 and it invariably established on the darker (south-facing) sides of panels.

Diplosoma macdonaldi (Herdman)

Although numerically of lesser importance than *Botryllus schlosseri,* this compound ascidian also became a conspicuous member of long-term fouling associations, with a similar spreading habit to *Botryllus.*

As indicated in the table below, infrequent settlement took place on monthly panels, but the combined records from all surfaces on which the species occurred suggest a main period of settlement from September to December.

TABLE 10.—Seasonal Settlement and Growth in *Diplosoma macdonaldi.*

IMMERSION (months)		PANEL WITHDRAWN	NO. SEPARATE COLONIES	AVERAGE SIZE (sq cm)
1	(L1)	November 1953	1	1·0
	(L1)	October 1954	5	1·0
	(L1)	November 1954	5	2·0
	(L1)	December 1954	6	2·5
2	(L1)	December 1954	? (coalescing)	20·0 (total)
3	(L1)	November 1953	? (coalescing)	30·0 (total)
	(L2)	November 1953	2	12·0/25·0
4	(L2)	October 1954	1	13·0
	(L1)	September 1955	2	6·0
6	(L2)	November 1954	1	15·0
	(L1)	November 1955	? (coalescing)	20·0 (total)
9	(L2)	May 1954	1	12·0

Growth in *Diplosoma* was more rapid than in *Botryllus* and colonies appeared more frequently on panels set at L1 than on those at L2. As with *Botryllus,* settlement took place on the darker sides of panels.

LONG-TERM ASSEMBLAGES

As the experimental series progressed, it became apparent that panels immersed for more than 6 months contributed little information on

the development of fouling assemblages. Much of the growth acquired by long-term panels, probably through an increasing susceptibility to wave action, stripped off, yielding bare areas on panel surfaces which immediately became available for colonization by new forms. This led to a lack of correspondence between any pair of long-term panels of similar immersion histories, whereas pairs of panels immersed 1, 2, and 4 months were fairly well duplicated as regards the variety and amount of growth carried.

Four-monthly panels, like those immersed for 2-monthly periods, were of value in observing the survival of earlier settlements under conditions of prolonged immersion. They also showed some of the effects previous settlements had on contemporary ones, and how dominant species varied on surfaces according to the duration and season of immersion.

JUNE TO SEPTEMBER (1954). This period covered the winter phase of minimum settlement and only some 60% of the total surface area of the panel was colonized. As nearly all forms settling during each individual month were present on the 4-monthly panel, its record was notable for the variety of species established. They were *Corella eumyota, Elminius modestus* (both co-dominant), *Botryllus schlosseri* (sub-dominant), *Molgula mortenseni, Pomatoceros terrae novae, Bugula* sp. nov., *Navicula grevillei,* and *Enteromorpha* sp. *Corella* had been the dominant form on monthly panels of June, July, and September, while *Elminius* settled abundantly in June, August, and September. Almost continuous settlement by these two species, throughout 3 of the 4 months in question, probably accounts for their dominance on the 4-month panel. *Botryllus* was not recorded from monthly panels until October and its prominence on the 4-month panel indicates an earlier and possibly a preferential settlement on the fouled surface. Both algal forms appeared in August and September.

OCTOBER TO JANUARY (1955). This panel, on withdrawal, showed great contrast to the June-September record. Its immersion overlapped the season of most intense fouling, and in bearing much closely-settled growth, displayed some competitive features in summer settlement. Fewer species were found on this panel than on any individual monthly panel of the period. Dominating the available surface were *Asterocarpa* and *Bugula* sp. Other species, less abundant, were *Corella, Botryllus, Bugula* sp. nov., and a few *Elminius* that were mainly confined to the panel borders.

The absence of several forms from this surface is noteworthy in view of their occurrence, often in large numbers, on monthly panels immersed during the period. Hydroids, which dominated surfaces in October, November, and December, algae, which were abundant components of October and November panels, serpulids, and *Elminius* which had settled densely in October and November, were all either absent or very sparsely represented. Of the two main components, *Bugula* sp. commenced to settle intensively in December, and *Asterocarpa* is presumed to have been a late-spring settling form. Establish-

ment and ultimate growth of these two species apparently was so great as to exclude from the surface many of the other forms settling both contemporaneously and beforehand.

As mentioned earlier, if *Elminius* had attached initially to the 4-month panel in as great numbers as to the monthly panels, it was surprising to find that so few barnacles persisted on prolonged immersion. It is not improbable that numerous colonies of *Bugula* sp., settling in December on both unoccupied surface and upon small barnacles, could have precluded further development of the barnacles, either by drastically reducing the food supply in their vicinity or by mechanically fouling their mobile opercular plates. Small barnacles killed by growth of a dense epizoic settlement of polyzoan colonies would be expected eventually to fall off, and the space they formerly occupied would be quickly colonized by further polyzoan larvae. Unlike members of the genus *Balanus, Elminius* barnacles have membranous bases, so that death and removal of animals from a surface seldom leaves any vestige by which a former colonization can be recognized. But if the low numbers of barnacles present on this panel at the end of January can be taken as an indication that some depletion took place, in the early summer, of barnacle populations which settled in the spring, any competitive reactions causing this seem more appropriately ascribed to *Bugula* sp. than to the other dominant summer-settling forms, the ascidians *Corella, Asterocarpa,* and *Botryllus.* For in many instances, barnacle populations were found overlaid by ascidians, both simple and compound, and apparently thriving, although only the smallest slit or interruption in ascidian tests permitted free communication with the water for cirral activity.

FEBRUARY TO MAY (1955). In that most forms settling during each month of this period were present, this 4-month panel resembled the one immersed from June to September. Settlement was moderately intense, the panel surfaces being approximately 70% colonized. Dominant were *Phialella quadrata,* which settled in April, and *Corella cumyota,* present on all monthly panels. Next in numerical importance were *Bugula* sp., *Elminius,* and *Hydroides norvegica.* Also present, but somewhat sparsely represented were *Asterocarpa cerea, Plumularia setacea, Sycon ornatum, Molgula mortenseni,* and *Spirorbis* sp.

The autumn reappearance of *Phialella quadrata* which had previously settled during the spring was displayed on all panels in position during April and May. There may be two possible explanations for this bi-ananual appearance of *Phialella.* First, the autumn settlement could have arisen from larvae developed as a result of the maturing of medusae originally released by colonies established in the preceding spring. Secondly, larval production may have been continuous from October to April, but settlement on surfaces prevented by the presence of *Bugula* colonies. In regard to the latter possibility, it must be noted that the decline of *Phialella* colonization in December coincided with the onset of dense *Bugula* settlement, while the decline of *Bugula* in April-May coincided with the reappearance of *Phialella.*

Other Long-term Immersions

The bulk of growth borne by panels immersed 6 months or more was usually composed of the ascidians *Asterocarpa, Botryllus,* and *Diplosoma.* These were joined by colonies of *Bugula* sp. when the period of immersion included the mid-summer months. On bare areas where clumps of ascidians had fallen off, growth consisted of those forms settling at the time when these areas became free.

The single panel from L1, which had been submerged 20 months (April 1954 to November 1955), bore two species, ? *Diadumene neozelanica,* and ? *Halichondria* sp., which had not appeared on any other panel. It seems that both of these became established after the panel had been in position some considerable time.

The long-term panels gave some indication of the longevity of the various species subsequent to their establishment on surfaces. As far as these investigations continued, and apart from repressive effects resulting from competitive factors, *Sycon ornatum, Cryptosula pallasiana, Pomatoceros terrae novae, Hydroides norvegica, Spirorbis* sp., *Elminius modestus, Asterocarpa cerae, Botryllus schlosseri,* and *Diplosoma macdonaldi* appeared to survive indefinitely. Colonies of both hydroids, *Phialella* and *Plumularia,* failed to persist more than a month after the most recent season of settlement, and only a few of the colonies of *Bugula* sp. established during the summer survived after June or July.

Differences in Fouling Between Sites

Of all factors contributing to environmental differences between Station L1 and L2, three are likely to have been of major importance.

Exposure. As L1 was on the southern side of the port, wave-action and turbulence resulting from prevailing north-easterly winds would be expected to be more severe at this position than at L2 on the opposite side of the port. Both sites were sheltered from the effects of winds from a south-westerly direction, L1 by the adjacent breakwater, and L2 by wharves and locally-moored shipping.

Tidal Currents. Current velocities at ebb and flood tides would have been greater in the vicinity of L1, which was within 50 yds of the port entrance fairway. Horizontal tidal movement would have been less marked at L2, which was some 600 yds opposite the entrance on the northern perimeter of the port.

Aspect. Although all panels at both stations were similarly orientated, the frame at L2 was placed beneath the wharf planking, and its panels would have been exposed to little direct sunlight during each day. L1, on the other hand, had an unrestricted northerly aspect and the north faces of panels were directly illuminated.

With the exceptions of the anemone and siliceous sponge from L1, all species recorded during the investigations were found at both stations, and the only consistent differences in fouling between L1

and L2 were quantitative ones. In general, the colonization of surfaces at L1 was more intense, and rates of growth appeared to be greater, the single exception being in the tendency for greater numbers of *Elminius* barnacles to settle at L2. At L1 there was a conspicuous preference by all forms except the algae for settlement on the south (darker) sides of panels—a trend which was less clearly defined on panels at L2.

No additional investigations were made to discover the reason for the heavier settlement and growth of species at L1. However, the proximity of this station to larval populations and nutrient material borne by water entering the port on the flood tide, and the possible effect of the prevailing north-easterly winds in concentrating the dispersal of larvae on the southern side of the port, may have been important contributory factors.

DISCUSSION

As settlement on surfaces was sampled at depths ranging from 1 to a maximum of 7 ft below E.L.W.S., it is possible that other records made at greater depths would differ from those obtained. Species naturally occurring within a wide range of depths would be represented on surfaces immersed at all included levels, but other forms normally may be limited to smaller ranges so that their appearance on panels outside these could be entirely fortuitous. Species which, in view of their abundance and regularity in seasonal settlement in both years examined, can be regarded as the most prominent fouling forms encountered, include *Navicula grevillei, Enteromorpha* sp., *Phialella quadrata, Plumularia setacea, Pomatoceros terrae novae, Hydroides norvegica, Elminius modestus, Bugula* sp. aff. *B. neritina, Cryptosula pallasiana, Corella eumyota, Asterocarpa cerea,* and *Botryllus schlosseri.* All these forms have been taken from the hulls of ships of draughts up to 23 ft, and with the exception of the algae and possibly the hydroid, they occcur on all areas of the underwater surfaces. Some regional zonation of fouling species does take place on ships, but it is more closely related to surface contour than to any vertical gradient in the occurrence of the different forms. This matter has been previously referred to by Pyefinch (1950) who observed that the water-line belt of algal fouling represented the only distinct example of regional differences in distribution of the common fouling organisms on the various parts of hulls. The panel immersion method may therefore be considered to give a reasonably accurate representation of seasonal settlement of the more common species of primary importance as ship-foulers. Densities of colonization and rates of growth, however, may vary with depth, and use of a single battery of test panels as in the present investigations, may produce figures only of relative value in these two respects.

Judging from the even distribution of species settling on panel surfaces, the size of panel used was adequate for fouling assess-

ments covering immersion periods of up to an average of 4 months, or 2 to 3 months in summer and 5 months over the winter. Unevenly increasing masses of growth associated with panels immersed for longer periods debarred any valid appraisal of the progressive development of aged fouling communities, for which larger panels would have been necessary. On some shorter-term panels, settlement of some forms, particularly barnacles and hydroids, tended to be somewhat more dense towards the edges and by the supporting brass channels. Because of this only the centre square decimetre was examined for quantitative data.

An outstanding feature of the experimental results was the influence of season on settlement and growth of organisms. Throughout the year a sequence of different forms appeared on newly-immersed surfaces, each individual species having a characteristic period during which larval settlement occurred as a result of seasonal rhythms in reproduction. This seasonal sequence of settlement accounts for much of the changing picture of dominance on surfaces immersed up to 1 or 2 months. Further, the nature of the fouling on such surfaces depends largely on both the time of year and duration of immersion, so that any reproducibility between fouling populations on duplicate surfaces becomes limited to similar immersion histories over corresponding seasons or parts of seasons. The influence of sea-water temperatures on growth has been demonstrated for *Phialella quadrata*, *Bugula* sp. aff. *B. neritina*, and *Corella eumyota*, greatest rates of growth being closely associated with higher annual temperatures. From the economic point of view, this intensifies the problem of a high rate of settlement over the summer months in that individual forms attain comparatively larger sizes within a short time.

Interpretation of the development of communities of organisms on panels immersed for long periods is complicated by differential growth rates of the attached forms, or by what Harris (1946) has termed "biological exclusion". This conveniently describes the process by which certain species, by virtue of their growth habits or density of settlement, suppress both the later establishment of certain other forms and continued growth in existing populations of earlier-settling groups. To such "exclusion" reactions arising from the dense development of *Bugula* colonies in summer might be attributed some depletion of spring-settling barnacle populations (and a retarding of growth in individuals) on 4- or 6-monthly panels withdrawn towards the end of the summer. In the same way, this polyzoan might have accelerated the decline of *Phialella quadrata* populations on panels in late December. Observations of the serpulid *Pomatoceros terrae novae* suggest that individuals settling on panels in the spring also suffered in competition for space with *Bugula* colonies later in the summer. By comparison, the second serpulid, *Hydroides norvegica*, commencing settlement in February, competed successfully with the polyzoan through the rapid growth of its calcareous tubes whose apertures projected well beyond the plane of basal attachment.

Two reasons can be advanced to account for the tendency shown by *Elminius* barnacles to settle in greater numbers upon surfaces which had been immersed for some time than on newly exposed surfaces. It is now well known that the texture of the surface has much influence on the density of barnacle settlement, greater settlements taking place on rough surfaces than on smooth ones. In the Lyttelton investigations, panels which had been immersed previously differed from clean ones, either in bearing other growths, or in winter months, films composed mainly of diatoms and particulate detritus. The presence of these films may have contributed to a surface texture more suitable for *Elminius* settlement than did the artificially-roughened surfaces of fresh panels. Secondly, Knight-Jones and Stevenson (1950) have demonstrated a gregarious tendency in *Elminius* settlement wherein significantly greater numbers of individuals attached to areas of surfaces which already bore barnacles than on similar adjoining areas which were bare. Thus, panels whose surface texture had been altered under conditions of prior immersion as well as those bearing earlier barnacle settlements, may both have been more favourable for colonization by young barnacles than the recently-exposed panels.

Peaks in the settlement of *Elminius modestus* during spring and autumn months were, as shown in Fig. 7, fairly well defined in each year. In their observations in Wellington Harbour, Ralph and Hurley (1952) found that on short-term blocks the heaviest *Elminius* settlements occurred in May (1949), and less intense settlements in June and the following April. This suggested to these authors that the main spawning period of *E. modestus* was in the autumn. According to their data (Table II, p. 7) barnacles were also present on test blocks withdrawn in October and November, but it is not stated whether these might have been members of earlier established populations or recent (spring) arrivals. In considering temperature as a factor determining settlement, Ralph and Hurley reasoned that because no settlement in October-November occurred at any intensity comparable to that in autumn when temperature ranges were approximately the same, this factor could not have been greatly important.

It may not be entirely valid to attribute a particular dense settlement of young barnacles to a certain limited period of intense adult spawning. As there is a planktonic phase, in the course of the life history, involving six successive developmental stages, factors which have much influence on the welfare of these free-living planktonic nauplii will obviously have an indirect bearing on their later success in attaining ultimate sessile status, no matter what intensity of spawning initially occurred. The Lyttelton investigations showed that at least some young barnacles were present on most monthly panels, and even during the summer, when no settlement was observed, cyprids, which may possibly have been of *Elminius* stock, could be found among the stems of polyzoan colonies. This possibility, together with Moore's (1944) New Zealand-wide record of adult *Elminius* specimens being found bearing nauplii within their mantle cavities at all times of the year, supports a contention that spawning may take place throughout

most if not the whole of the year. Autumn and spring peaks in the intensity of larval settlement then, may arise from the influence of similarly changing conditions affecting the planktonic stages and of such, autumn and spring maxima in phytoplankton production may be of the most appropriate significance. As far as the author is aware, feeding by the nauplii of *E. modestus* has not so far been reported, but most workers have recognized that typical cirripede nauplii do feed. It would be reasonable to suppose, therefore, that an abundance of food for feeding larvae would contribute to the survival and completed development of a higher proportion of those released at spawning. A critical investigation has been made by Barnes (1956) of a similar question of year to year variations in the development of larval populations of *Balanus balanoides,* a common shore barnacle in the Firth of Clyde which settles during April. Possible causes of catastrophic reductions, in certain years, in the numbers of cyprids following the liberation of early stage nauplii, were examined and it was suggested that abnormalities in the spring diatom outburst during these "failure" years were related to the depleted late stage larval populations by alterations of the available food supply.
between Lyttelton and Wellington, is cordially acknowledged.

While enabling definition to be made of the basic characteristics of marine fouling at Lyttelton, the scope of this survey has permitted little beyond an introduction of a number of secondary problems concerning the various species. Year to year variations in reproductive cycles and settlement, the causes of seasonal fluctuations in *Elminius* settlement, sea temperature and growth-rate relationships, and "biological exclusion" factors in competitive settlement, are all questions requiring further investigation, and for which more extensive observations than at present available, will be necessary.

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THE IMMATURE STAGES OF *ERIOCOCCUS ORARIENSIS* HOY (HOMOPTERA, COCCOIDEA)

By J. M. Hoy, Entomology Division, Department of Scientific and Industrial Research, Palmerston North

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Summary

The morphology of the immature stages of *Eriococcus orariensis* Hoy was examined to provide a basis for life history studies on this insect, which is the causal organism of manuka blight in New Zealand. A number of structures were measured, the only measurement of value in distinguishing between stages being the combined length of the tibia and tarsus of the posterior leg. These measurements were used as a basis for the selection of characters allowing all stages of the insect to be readily identified. The type and distribution of sessile pores and tubular ducts proved to be a reliable character for separation. In *E. orariensis* there are three stages in the female and five stages in the male. Descriptions of the immature stages are based on an examination of forty specimens in each stage.

Trilocular pores occur in the first-stage nymph of *E. orariensis*; this is the first record of such pores in the Eriococcidae. Unusual types of tubular ducts were found in first-stage nymphs and second-stage males and females. A statistical examination was made of variation in leg length within instars and between instars.

INTRODUCTION

Eriococcus orariensis, the causal organism of manuka blight, has become established by means of natural dispersion and deliberate transfer in almost all large stands of *Leptospermum scoparium* Forst. throughout New Zealand. This insect has been studied in an attempt to elucidate its role in killing manuka and to provide fundamental information which may be of use in future attempts at biological control of noxious weeds. As far as the writer is aware, a close investigation of the immature stages and the life history of a species of the genus *Eriococcus* has not been made previously. A detailed description of the adult male and female of *Eriococcus orariensis* was given in a previous paper (Hoy, 1954).

Under North Island conditions, it was apparent that this insect had more than one generation per year, but, because of the large size of individual colonies, there is considerable overlapping between generations. This factor made it difficult to follow the life history on heavily infested plants. *E. orariensis* establishes in bark crevices and under exfoliated bark on the host plant, thus it is impossible to study individual specimens over a prolonged period without disturbing their surroundings. Once the surrounding bark is removed, the insect usually dies within a short period of time, so that the life history of a particular individual cannot be followed from egg to maturity. The method finally

selected for life history studies involved the removal of population samples at regular intervals from specimen plants infested with newly hatched first instar nymphs. Because of their small size, all specimens were mounted for microscopic examination. This study of the immature stages of *E. orariensis* was undertaken to find characters which would allow the separation of all stages both of the male and female in microscope preparations.

MATERIALS AND METHODS

All insect specimens examined in this study were collected from an isolated stand of *L. scoparium* in the Shannon district. This area had been artificially infested with the insect five years previously. Due to the large amount of material to be mounted on microscope slides, collection of material in the field was spread over a period of one week. During this time all stages of the insect were present on plant material collected. Twigs were taken at random throughout the area of infestation. A total of 107 slides, each containing approximately 30 individuals, were made using Berlese's fluid as a mountant. Specimens were mounted in groups according to the apparent stage, thus slides were made containing first instar nymphs fixed to host, first instar nymphs moving free on plant, second instar nymphs fixed to host, second instar nymphs moving free, and second instar males removed while constructing puparia. The difficulties encountered in mounting large numbers of such organisms further randomizes the selection of individuals suitable for measurement.

Measurements were taken in a darkened room under standardized conditions by projection through a microscope using a prism. Care was taken to ensure that optical distortion was kept to a minimum. Measurements on the projected image were made with a pair of dividers. This method allowed the handling of large numbers of specimens with a minimum of fatigue and consequent operator error.

Morphological descriptions of the various instars were made on unstained specimens mounted in Berlese's fluid and examined under phase contrast.

IMMATURE STAGES OF *E. orariensis*

Coccids offer few characters suitable for measurement, since the amount of sclerotization is not large, and distortion and stretching of intersegmental membranes is likely to occur during mounting.

In the initial stages of measurements, 582 specimens of the immature stages of *E. orariensis* other than male pupae and prepupae were measured for the following characters: Overall length from frons to the tip of the anal lobes, exclusive of the anal lobe setae: overall width at the widest part of the body; the total length of the antenna; and the combined length of the tibia, tarsus, and claw. Measurements were made at a degree of magnification allowing separation into classes 6μ apart.

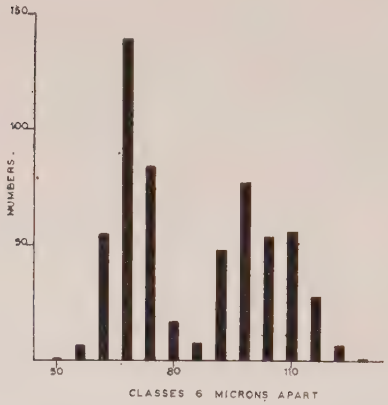

FIG. 1.—*Eriococcus orariensis*, immature stages other than male pupae and prepupae—Frequency distribution of combined length of tibia, tarsus, and claw (582 specimens).

The frequency distribution of measurements of the combined length of the tibia, tarsus, and claw of the first series specimens is shown in Fig. 1. While a relatively clear separation was obtained between first and second instar, there was little evidence in the bulk sample of differences between males and females at the second stage. During measurements, the apparent stage of each specimen was noted and the sample was further examined on this basis. The frequency distribution of tibia, tarsus, and claw measurements under stage classes is shown in Fig. 2. Second instar males, identified as such by removal from the plant while they were constructing puparia, showed a peak in the 110 μ class. Fixed second instar individuals which presumably consisted of both male and female forms showed a peak in the 98 μ class.

The frequency distribution of total antennal length is shown in Fig. 3. No clear-cut separation of instars could be obtained from these measurements, due partly to the range of variation that occurs in antennal length and partly to the difficulty of obtaining accurate overall measurements, due to distortion of the antenna in preparation of microscope mounts. The frequency distribution of overall length and width is not shown, but these characters were of little use in distinguishing between instars in the sample measured.

The only measurements that appeared likely to aid in differentiating between the nymphal stages were those taken on the combined length of the tibia, tarsus, and claw. The angle at which the claw lay in relation to the tarsus led to difficulties in measurement, so that the claw was omitted from a second series of measurements. The tibia and tarsus appeared the least susceptible to distortion in mounting, allowing a greater degree of precision to be obtained. A further series of 300 specimens was measured for combined length of tibia and tarsus at a higher degree of magnification, which allowed classes to be separated

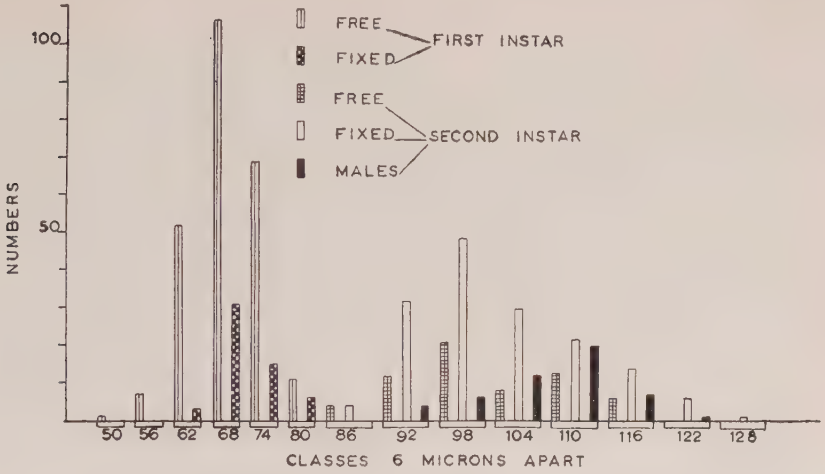

FIG. 2.—*Eriococcus orariensis,* immature stages other than male pupae and prepupae—Frequency distribution of combined length of tibia, tarsus, and claw in stage classes (582 specimens).

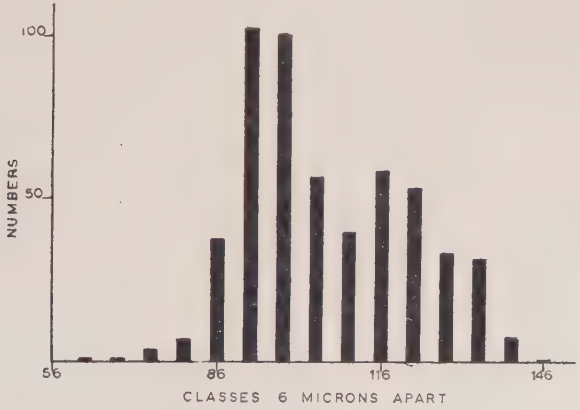

FIG. 3.—*Eriococcus orariensis,* immature stages other than male pupae and prepupae—Frequency distribution of total antennal length (582 specimens).

by 1·5 μ. The frequency distribution of this series of measurements is shown in Fig. 4. Tibio-tarsal length of second instar females showed a peak in the 81·5 μ class and that of second instar males in the 99·5 μ class. A small amount of overlap occurred in the 89 μ class.

Following the demonstration of the usefulness of tibio-tarsal measurements for distinguishing instars, a further range of specimens was selected for more detailed measurement. A total of 40 specimens in each instar was chosen, 20 immediately after hatching or moult and 20

FIG. 4.—*Eriococcus orariensis,* immature stages other than male pupae and prepupae—Frequency distribution of combined length of tibia and tarsus (300 specimens).

at the end of the instar. The criterion accepted for impending moult was the presence of the coiled rostral filaments of the next stage. It is possible that some of the specimens at moult were in reality pharate forms of the next stage (Hinton, 1946), but since their tibio-tarsal measurements corresponded to those at eclosion they were regarded, for the purposes of this study, as belonging to the previous instar. Measurements were made of overall length and width, length of individual antennal segments, length of individual leg segments except for a combined measurement of trochanter and femur. A similar range of measurements for comparative purposes was made on 20 mature adult females collected from the same locality. These measurements are detailed in the description of the various instars given below.

The developmental stages of *E. orariensis* are similar to those of the majority of coccid species in which the life history has been studied. The stages are illustrated by the series of photomicrographs (Fig. 5). They are as follows:

FEMALE

(1) Egg (Fig. 5 (1)).

(2) First-stage nymph.

(a) Crawler, motile a short time after eclosion (Fig. 5 (2)).

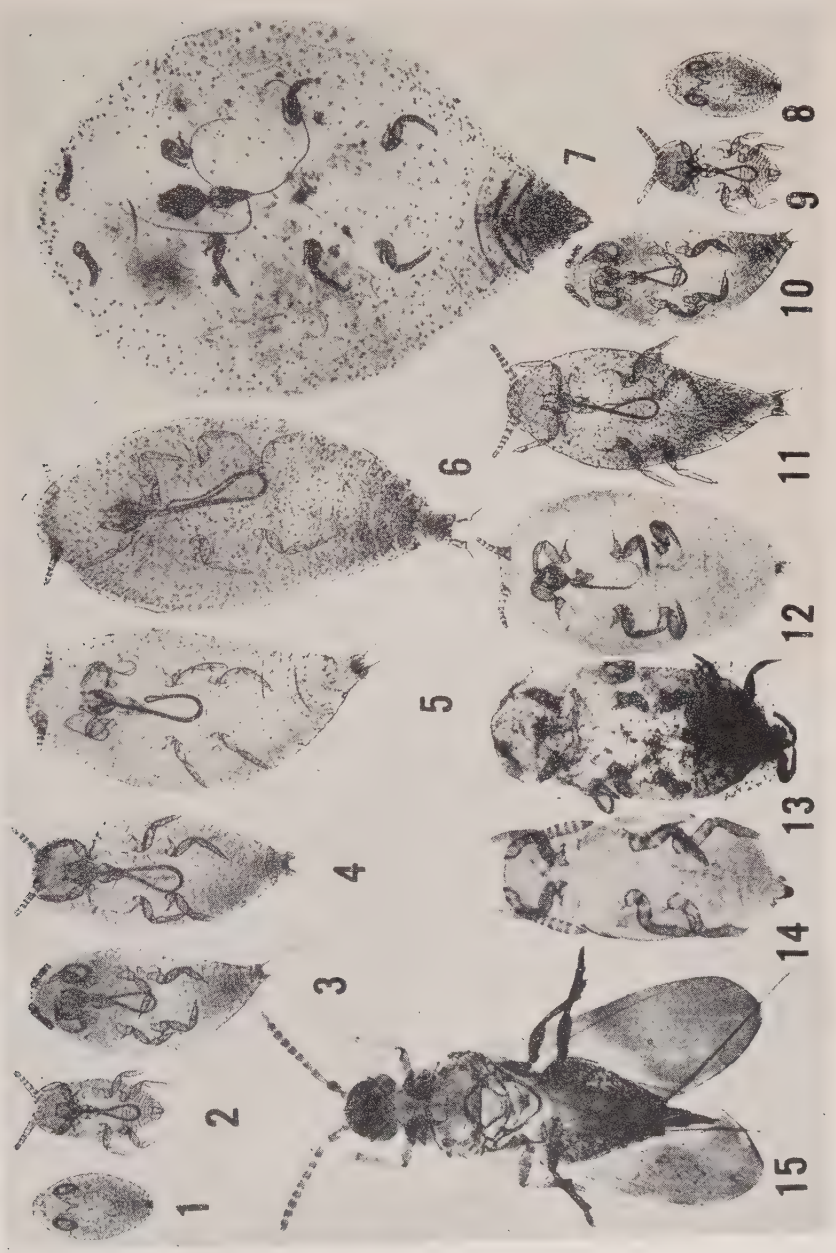

FIG. 5.—Stages in the life history of *Eriococcus orariensis*. For explanation of individual photomicrographs 1 to 15 see text. Magnification $\simeq \times 55$.

(b) Fully grown, showing the coiled rostral filaments of the next instar (Fig. 5 (3)).

(3) Second-stage nymph.
(a) Immediately after moult (Fig. 5 (4)).
(b) Fully grown, showing the coiled rostral filaments of the adult female (Fig. 5 (5)).

(4) Adult female.
(a) Shortly after moult from the intermediate stage. (Fig. 5 (6)).
(b) At maturity (Fig. 5 (7)).

MALE

(1) Egg as for female (Fig. 5 (8)).

(2) First-stage nymph. Indistinguishable from female of same stage.
(a) Crawler (Fig. 5 (9)).
(b) Fully grown (Fig. 5 (10)).

(3) Second-stage nymph.
(a) Shortly after moult, before settling on the host plant Fig. 5 (11)).
(b) Fully grown, at time of construction of puparium (Fig. 5 12)).

(4) Prepupa. Shedding skin of the second stage (Fig. 5 (13)).

(5) Pupa (Fig. 5 (14)).

(6) Adult male (Fig. 5 (15)).

Morphology

EGG (Fig. 5 (1 & 8))

The egg is oval in general outline, with broadly rounded ends. At oviposition the average overall length is 285 μ (range 250 to 384) and the average overall width 163 μ (range 133 to 186) (50 specimens). The first-stage nymph is fully developed at oviposition, and details of the body, particularly the coiled rostral filaments, can be seen through the transparent chorion.

FIRST-STAGE NYMPH AT ECLOSION (Fig. 5 (2 and 9))

The body is ovoid, truncate at the anal end, eyespots are prominent, not showing any marked pigmentation. The average overall length, exclusive of the anal lobe setae, is 356 μ (range 288 to 400). The average overall width at widest point is 151 μ (range 147 to 160) (20 specimens). The derm shows little evidence of sclerotization, being mem-

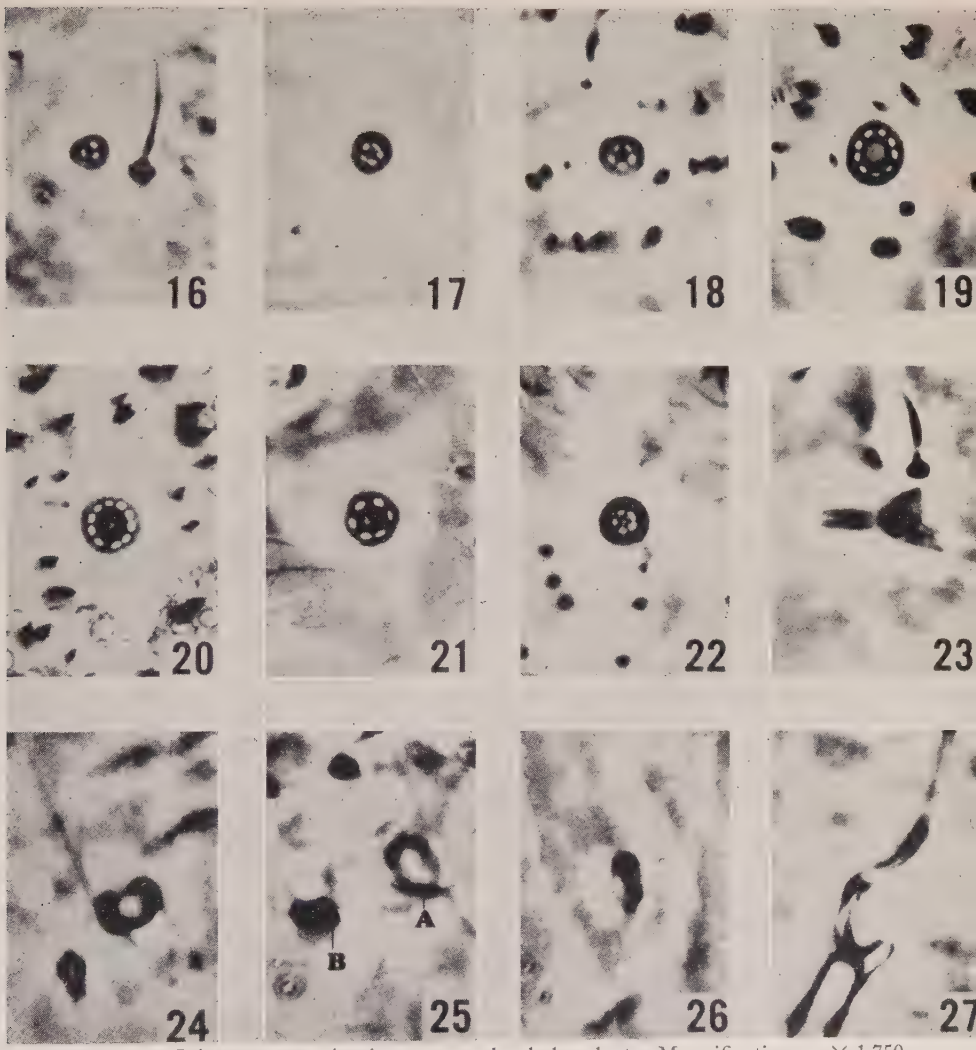

FIG. 6.—*Eriococcus orariensis*, pores and tubular ducts. Magnification $\simeq \times 1{,}750$.

(16) Trilocular pore—first stage nymph.
(17) Quinquelocular pore—second stage male.
(18) Quinquelocular pore—second stage female.
(19) Multilocular pore—pupal male.
(20) Multilocular pore—prepupal male.
(21) Pore with six loculi—pupal male.
(22) Quniquelocular pore—adult female.
(23) Tublar duct—first stage nymph.
(24) Inner extremity, tubular duct—second stage male.
(25) A—opening to large tubular duct. B—opening of small bifurcate tubular duct—second stage male.
(26) Double opening of tubular duct—second stage female.
(27) Inner extremity, tubular duct, adult female.

branous but slightly nodulose, particularly towards the lateral margins on the dorsal aspect of the cephalic and thoracic regions. On the ventral aspect of the abdominal segments there are a large number of spicules. These spicules appear to be produced by a folding of the derm. Spicules are present to a lesser degree on the venter of the meso- and meta-thoracic segments and on the dorsal aspect of the abdominal segments.

On the ventral surface there are a number of small trilocular disk pores (Fig. 6 (16)). These pores are subcircular in shape, 3·5 μ wide, with a definite sclerotized margin and 3 separate and distinct loculi. They differ from the type of trilocular pore commonly observed in Pseudococcidae in that the radii are not curved and are always joined at the centre. Ferris (1955) stated that trilocular pores are not known to be present in any species that belongs definitely to the Dactylopiidae now Eriococcidae (Ferris, 1957). These pores have also been observed in the first nymphal stage of *Eriococcus leptospermi* Mask. and in an undescribed species of *Eriococcus* taken on *Leptospermum* in Australia. They have not been observed in the first nymphal stage of any other species of *Eriococcus* examined to date in New Zealand.

Trilocular pores occur, 1 towards each lateral margin on the venter of abdominal segments 3 to 6 inclusive, a pair each on the meta- and meso-thoracic segments between the coxae, and a further pair between the points of attachment of the antennae. No other type of pore was observed on the ventral surface.

Tubular ducts (Fig. 6 (23)) are present on the dorsum; these ducts have a very small cup at their inner extremity from which a relatively short filamentous tube leads to the lumen of the associated gland. The opening to the exterior is unusual in that the duct is bifurcated close to the surface of the cuticle and the duct has a pair of circular orifices each raised above the surface on a minute cone-like projection. A pair of these ducts is present, 1 towards each lateral margin on abdominal segments 1 to 7 inclusive, also on the lateral margins of the pro-, meso-, and meta-thoracic segments and a pair just posterior to the level of the eye spots.

On both the ventral and dorsal surfaces the pores and ducts respectively occur in line with the transverse row of setae on each segment.

The pro-thoracic spiracles are normal in appearance and are accompanied by a single trilocular pore. The meso-thoracic spiracles are not accompanied by a disk pore.

On the dorsum of abdominal segments 1 to 7, and on each of the thoracic segments, there is a single transverse row of 6 setae. Two transverse rows of 4 setae occur posterior to the level of the eyespots. Anterior to the eyespots there are 8 marginal setae as well as 1 seta on either side of the median line just posterior to the anterior margin. Abdominal segments 1 to 7 and the thoracic segments carry a marginal seta on either side, these together with the outer setae of the transverse row give the appearance of 2 marginal setae on the lateral margin of each segment. All these setae are fine, sharp tipped, and of moderate length, becoming slightly longer on the posterior abdominal segments.

On the venter, each of abdominal segments 3 to 6 carries a transverse row of 4 to 6 longer but more slender setae; a pair of similar setae occur on abdominal segments 1 and 2. The meso- and meta-thoracic segments have a pair of setae between the coxae. On the pro-thoracic segment there is a small seta associated with each spiracle. Three transverse pairs of setae occur along the medial line in the cephalic region.

Antennae of the first-stage nymph have 6 segments; the length of each segment is given in Table 1. Segment 1 has a moderate length seta on the inner face; segment 2 has a similar seta; segment 3 has a moderate length seta on the inner ventral face, and a short seta on dorsal face; segment 4 has a longer seta on the ventral face; segment 5 has 1 long seta on the ventral face, 1 moderate length seta on the inner face, and 2 fine setae on the dorsal face; the terminal segment carries a strong seta on the inner face towards the base of the segment and another towards the apex, a large seta near the mid-point on the outer face, and another half-way between that seta and the apex, 1 long seta on the mid-dorsal face, and 2 long and 1 short apical setae.

TABLE 1.—*Eriococcus orariensis*—First Stage Nymph; Length of Antennal Segments at Eclosion, and When Fully Grown (20 Specimens at Each Stage).

(Measurements in μ.)

	First	Second	Third	Fourth	Fifth	Sixth	Total
At eclosion							
Mean	14·9	13·8	20·6	11·2	11·5	18·5	90·5
Range	12·0 to 17·0	12·0 to 15·5	18·5 to 23·0	9·0 to 14·0	9·0 to 14·0	17·0 to 20·0	81·5 to 97·0
Fully grown							
Mean	16·2	14·5	21·2	11·4	11·4	18·3	92·8
Range	15·0 to 17·0	12·0 to 15·5	20·0 to 23·0	9·0 to 14·0	9·0 to 14·0	17·0 to 20·0	84·5 to 95·5

The rostrum consists of 2 segments, 2 large labial setae occur at the distal end and a number of shorter setae are also present. At eclosion the rostralis is coiled within the crumena.

The legs are well developed and normal, the length of the various segments is given in Table 2. The chaetotaxy of the anterior leg is as follows: coxa has 1 short and 2 longer setae on the ventral face, on the dorsal face there are 2 long setae, 1 toward each of posterior and anterior faces. On the trochanter there are a pair of sensoria on the ventral face which also carries a long conspicuous seta and a short seta towards the distal portion, on both the anterior and posterior

TABLE 2.—*Eriococcus orariensis*—First Stage Nymph; Length of Leg Segments at Eclosion, and When Fully Grown (20 Specimens at Each Stage). (Measurements in μ.)

	Legs					
	Anterior		Middle		Posterior	
	Mean	Range	Mean	Range	Mean	Range
At eclosion						
Coxa	16·3	14·0 to 17·0	16·6	15·5 to 18·5	17·7	15·5 to 20·0
Trochanter-femur	49·4	44·5 to 54·0	51·5	47·5 to 54·0	52·2	46·0 to 57·0
Tibia	24·6	21·5 to 26·0	25·2	21·5 to 27·5	25·2	21·5 to 29·0
Tarsus	30·8	27·5 to 32·0	32·6	29·0 to 35·5	34·2	31·0 to 35·5
Claw	14·9	14·0 to 17·0	15·2	14·0 to 17·0	15·7	14·0 to 17·0
Overall length	135·8	129·0 to 143·0	140·9	129·0 to 147·5	145·8	137·0 to 158·5
Fully grown						
Coxa	16·2	14·0 to 17·0	17·1	15·5 to 18·5	17·2	15·5 to 20·0
Trochanter-femur	52·6	51·0 to 54·0	53·1	51·0 to 55·5	54·3	51·0 to 57·0
Tibia	24·5	23·0 to 26·0	25·4	23·0 to 29·0	26·0	24·5 to 27·5
Tarsus	32·9	31·0 to 37·0	34·3	31·0 to 37·0	36·2	34·0 to 40·0
Claw	14·2	12·5 to 15·5	15·4	14·0 to 17·0	15·5	14·0 to 17·0
Overall length	140·2	135·5 to 146·0	145·1	140·0 to 154·0	148·9	140·0 to 154·0

faces there is a moderate length seta. On the ventral face of the femur are 2 short setae, 1 near the base and 1 near the distal end. The tibia has 1 moderate length seta near the distal end on the posterior face and in a similar position a short seta on the dosal face. On the tarsus there is a pair of moderate length setae on each lateral face and a similar seta on the mid ventral surface. The tarsal digitules are approximately 1½ times the length of the claw and have an expanded cone-shaped tip. The ungual digitules have a similar tip and are about the same length as the claw which has a minute denticle. The middle and posterior legs have a similar setal pattern to the foreleg.

The anal ring is well developed and poriferous with 6 anal ring setae, a single slender seta is present on either side of the anal ring on the ventral surface. The anal lobes are weakly sclerotised, subconical in shape. The anal lobe setae are about 3·5 times the length of the lobes. On the inner margin of each lobe there is a pair of stout blunt spines, on the outer margin one shorter and more slender spine, on the ventral surface a slender seta approximately equal in length to the lobes.

FULLY GROWN FIRST STAGE NYMPH (Fig. 5 (3 and 10))

Body shape more or less pyriform, about 1·7 times longer and 1·9 times broader than at eclosion. The actual dimensions of 20 specimens being: average length, 588 μ (range 500 to 680), average width 283 μ

(range 240 to 313). The derm is still membranous, but it is stretched thin and there is no sign of the nodulose condition which is marked at eclosion. The segmentation of the abdomen is not so obvious as at eclosion. The lengths of the individual antennal segments show the same range of variation as those of the newly hatched nymph (Table 1). Differences were noted in the length of segments in the legs (Table 2); the significance of these differences is discussed later.

The morphological features of the first instar have been described in some detail, to serve as a basis for separation of the later stages, using characters that are not dependent on measurement. Descriptions of the later stages are confined in general to characters allowing such separations to be made.

Although pharate forms of both the second stage male and female were carefully examined, no sex differences could be found in first stage nymphs.

SECOND STAGE MALE AT ECLOSION (Fig. 5 (11))

The body is elongate, oval, relatively broad at base of the anal lobes, the eyespots are still prominent, showing little sign of pigmentation. The average overall length exclusive of anal lobe setae is 700 μ (range 633 to 788) and the average overall width is 305 μ (range 267 to 368) (20 specimens). There is no evidence of any marked sclerotisation, the derm being membranous without the nodulose appearance of the first stage at eclosion. Fine spicules occur on the mid-portion of the venter of the meso- and meta-thoracic and abdominal segments as well as the ventral face of the anal lobes. Coarser spicules occur on the dorsum of the last 2 abdominal segments.

One of the most noticeable features of the second stage male is the increased number of sessile pores on the venter as compared with the first stage nymph. These pores are almost entirely quinquelocular. The quinquelocular pores (Fig. 6 (17)) are circular in outline, about 3·5 μ across, the margin is strongly sclerotised, the radii are short, and the central cell prominent. On the ventral surface, abdominal segment has 1 row of 4 such pores; segment 2 has 6; segment 3 has 8 quinquelocular pores, the outer pore on each lateral margin commonly has 6 or more loculi; segment 4 has 4 quinquelocular and 2 pores with a variable number of loculi between 5 and 10; segment 5 has the same number of pores as segment 4; segment 6 has 4 quinqueloculars, and segment 7 has a pair. The meta-thoracic segment has 4 quinquelocular pores, a pair between the coxae and 1 towards each ventro-lateral margin; there are 6 quinquelocular pores on the meso-thoracic segment and a moderate number of similar pores on the pro-thoracic and cephalic regions. On the dorsal surface there is a moderate number of tubular ducts with cup-shaped inner extremities (Fig. 6 (24 and 25A)). The cup is relatively shallow and wide and the tube to the exterior much shorter than that seen in the adult female. In addition to these relatively large tubular ducts, there are

TABLE 3.—*Eriococcus orariensis*—Second Stage Males; Length of Antennal Segments at Eclosion, and When Fully Grown (20 Specimens at Each Stage).

(Measurements in μ.)

At eclosion	First	Second	Third	Fourth	Fifth	Sixth	Seventh	Total
7-segmented forms:								
Mean	17·7	17·7	20·6	16·0	14·2	14·6	22·1	123·0
Range	17·0 to 18·5	17·0 to 18·5	17·0 to 23·0	14·0 to 20·0	12·5 to 15·5	12·5 to 15·5	20·0 to 23·0	114·0 to 129·5
6-segmented forms:								
Mean	18·5	18·2	28·9	13·8	13·9	22·0	—	114·9
Range	17·0 to 21·5	17·0 to 18·5	24·5 to 34·0	12·5 to 15·5	12·5 to 15·5	20·0 to 23·0	—	106·0 to 123·0
Fully grown								
7-segmented forms:								
Mean	19·1	17·8	20·3	16·3	13·4	13·2	21·7	121·3
Range	15·5 to 21·5	15·5 to 20·0	17·0 to 23·0	14·0 to 20·0	11·0 to 15·5	11·0 to 15·5	20·0 to 24·5	115·5 to 128·0
6-segmented forms:								
Mean	19·1	18·6	32·5	13·2	13·2	20·9	—	118·0
Range	18·5 to 21·5	17·0 to 21·5	27·5 to 38·5	12·5 to 15·5	12·5 to 15·5	18·5 to 23·0	—	109·5 to 126·5

a number of extremely small ducts towards the lateral margins, these ducts have a bifurcated opening (Fig. 6 (25B)) similar to those of the first stage. A small number of quinquelocular pores occur near the lateral margins of the dorsum.

The setae of both the venter and the dorsum are arranged in regular transverse rows, particularly on the abdominal segments. Setae on the ventral surface are slender and of moderate length, those of the dorsum are shorter and broader in the base.

The antennae of the second stage male have a variable number of segments, 68% of specimens measured having 7 segments and the remainder 6 segments. The extra segment arises from a division in segment 3, as can be seen in Table 3 which sets out the length of the antennal segments in the second stage male. The setae of the antennae offer no characters allowing separation of second stage males.

The legs are well developed, the length of the various segments is shown in Table 4. The anal lobes are short, conical and not strongly sclerotised. Each lobe carries 2 stout blunt spines on the inner face, and a shorter spine on the external face near the base, on the ventral face there is a long slender seta towards the distal end and a pair of shorter setae towards the base. The apical setae are 3 to 4 times the length of the lobes. The anal ring is well developed and poriferous, 6 anal ring setae are present.

TABLE 4.—*Eriococcus orariensis*—Second Stage Male; Length of Leg Segments at Eclosion, and When Fully Grown (20 Specimens at Each Stage).

(Measurements in μ.)

	Legs					
	Anterior		Middle		Posterior	
At eclosion:	Mean	Range	Mean	Range	Mean	Range
Coxa	24·8	21·5 to 29·0	26·0	23·0 to 29·0	26·8	24·5 to 29·0
Trochanter-femur	73·1	69·0 to 77·0	74·3	69·0 to 80·0	76·9	71·0 to 81·5
Tibia	39·4	35·5 to 43·0	41·2	38·5 to 46·0	42·3	38·5 to 46·0
Tarsus	52·9	49·0 to 57·0	55·8	54·0 to 58·5	57·4	54·0 to 60·0
Claw	19·2	18·5 to 20·0	19·7	18·5 to 21·5	20·5	20·0 to 21·5
Overall length	209·4	195·5 to 218·5	216·8	206·0 to 231·0	223·8	212·0 to 234·0
Fully grown:						
Coxa	24·5	21·5 to 28·0	25·8	21·5 to 29·0	26·2	23·0 to 27·0
Trochanter-femur	71·8	68·0 to 78·5	73·4	71·0 to 80·0	76·0	72·5 to 80·0
Tibia	38·9	37·0 to 41·5	39·5	38·5 to 41·5	41·8	37·0 to 44·5
Tarsus	54·0	52·0 to 55·5	55·7	54·0 to 58·5	56·8	54·0 to 60·0
Claw	18·6	17·0 to 20·0	20·0	18·5 to 21·5	20·3	18·5 to 21·5
Overall length	207·7	200·0 to 218·5	214·2	204·5 to 226·0	220·9	211·0 to 229·0

Second Stage Male, Fully Grown (Fig. 5 (12))

Body shape is oval, the average overall length is 886 μ (range 727 to 973), the overall width 386 μ (range 340 to 440) (20 specimens). The derm is distended, the anal lobes not prominent. The antennal segments (Table 3) show a similar range of variation as at eclosion. The average overall length of the legs (Table 4) is shorter than at eclosion.

Intermediate Female at Eclosion (Fig. 5 (4))

Body shape is elongate, oval, the anal lobes are more prominent than those of the second stage male. The average overall length is 649 μ (range 600 to 707), the average overall width is 287 μ (range 260 to 333) (20 specimens). Eyespots are present but are not so prominent as those of the second stage male. Except for the anal lobes, the derm is not strongly sclerotised, it retains the nodulose appearance of the first stage nymph not only on the dorsum but also on the ventral face of the cephalic region. Spicules on the venter more prominent than those in second stage male, dorsal spicules are much reduced and confined to abdominal segments 6 and 7.

The sessile pores of the venter (Fig. 6 (18)) are almost all quinquelocular about 3·5 μ across. On the pro-thoracic segment pores with 7 loculi are found occasionally. On the abdominal segments, pores with 6, 4, and sometimes 3 loculi are found on rare occasions. The quinquelocular pores are similar to those of the second stage male. There are considerably fewer pores on the venter than on that of the second stage male. Abdominal segment 1 has a pair of pores, 1 situated near each lateral margin, abdominal segments 2 to 5 inclusive have a pair of pores, each situated approximately half-way between the mid line and the margin of the segment. A pair of pores is situated on each of the meta- and meso-thoracic segments, on the pro-thoracic and cephalic regions there are small numbers of pores towards the lateral margins.

The tubular ducts on the dorsum open to the surface on an elongate oval or eight-shaped plate (Fig. 6 (26)), there appear to be 2 openings to each duct, the inner extremity of the duct is very little broader than the duct, the filamentous tube leading to the gland lumen appears to be quite short. There are relatively few tubular ducts compared with the adult female, the ducts are arranged in line with the transverse rows of dorsal setae. Each meta-thoracic and pro-thoracic spiracle is accompanied by a pair of quinquelocular pores.

The ventral abdominal setae are similar to those of the second stage male, the setae are slender and of moderate length, arranged in tranverse rows, one row per segment. The marginal setae are shorter and stouter but there is no prominent marginal fringe of setae. Setae of the dorsum are also arranaged in a single tranverse row per segment. On the dorsum of the penultimate abdominal segment towards each

TABLE 5.—*Eriococcus orariensis*—Intermediate Female; Length of Antennal Segments at Eclosion, and When Fully Grown (20 Specimens at Each Stage).

(Measurements in μ.)

	First	Second	Third	Fourth	Fifth	Sixth	Total
At eclosion							
Mean	19·1	18·0	25·4	13·7	13·8	21·8	111·5
Range	17·0 to 20·0	17·0 to 18·5	23·0 to 29·0	12·5 to 15·5	12·5 to 17·0	20·0 to 23·0	107·5 to 115·5
Fully grown							
Mean	19·8	18·6	26·3	13·7	13·5	21·4	113·2
Range	18·5 to 21·5	17·0 to 20·0	24·5 to 29·0	12·5 to 15·5	12·5 to 15·5	20·0 to 23·0	107·5 to 120·0

lateral margin is a stout peg-like blunt-tipped seta, the presence of these setae readily distinguishing the intermediate female from the second stage male. Similar setae occur in the adult female.

The antennae are slightly shorter than those of the second stage male and are always 6-segmented. The length of the segments is shown in Table 5. The arrangement of setae is similar to that of the antennae of the first stage nymph. The length of the leg segments is shown in Table 6.

The anal lobes are proportionately longer than those of the second stage male. The arrangement of anal lobe setae is similar to that of the second stage male but the terminal setae are usually only $2\frac{1}{2}$ to 3 times the length of the lobes. The anal ring is poriferous with 8 anal lobe setae which are longer than the length of the anal lobes.

INTERMEDIATE FEMALE, FULLY GROWN (Fig. 5 (5))

Body shape is more or less pyriform, the average overall length is 866 μ (range 700 to 993), the average overall width is 434 μ (range 327 to 520) (20 specimens). Although the derm is thin and membranous, it still shows evidence of nodulation on the lateral margins. The length of the antennal segments (Table 5) is similar to the length at eclosion. As in the case of the first stage nymph, the average overall length of each leg (Table 6) has increased during the stadium, the apparent increase is confined to the length of the tarsus and the trochanter-femur.

PREPUPAL MALE (Fig. 5 (13))

Body shape is oval with broadly based conical anal lobe projections, the leg and wing buds are weakly developed, the antennae short and stout. The average overall length is 796 μ (range 586 to 959), the

TABLE 6.—*Eriococcus orariensis*—Intermediate Female; Length of Leg Segments at Eclosion, and When Fully Grown (20 Specimens at Each Stage). (Measurements in μ.)

	Legs					
At eclosion	Anterior		Middle		Posterior	
	Mean	Range	Mean	Range	Mean	Range
Coxa	21·1	18·5 to 24·5	20·6	20·0 to 23·0	21·2	20·0 to 24·5
Trochanter-femur	57·7	52·5 to 60·0	59·4	55·5 to 61·5	61·4	58·5 to 64·5
Tibia	30·9	29·0 to 34·0	31·8	29·0 to 34·0	33·7	31·0 to 37·0
Tarsus	43·7	41·5 to 46·0	46·3	43·0 to 51·0	48·3	44·5 to 52·5
Claw	18·2	17·0 to 20·0	18·9	17·0 to 20·0	19·1	17·0 to 21·5
Overall length	171·4	165·5 to 180·0	176·8	172·5 to 183·0	183·4	177·0 to 194·0
Fully grown						
Coxa	20·2	18·5 to 21·5	21·2	20·0 to 23·0	21·1	18·5 to 23·0
Trochanter-femur	60·9	58·5 to 64·5	60·9	57·0 to 64·5	61·7	58·5 to 66·0
Tibia	31·1	29·0 to 34·0	33·4	31·0 to 37·0	33·7	31·0 to 37·0
Tarsus	46·2	43·0 to 49·0	48·2	44·5 to 51·0	50·3	47·5 to 52·5
Claw	18·6	15·5 to 21·5	18·9	17·0 to 20·0	19·2	17·0 to 20·0
Overall length	176·8	171·0 to 183·0	182·5	175·5 to 192·5	185·8	178·5 to 194·0

average overall width is 320μ (range 244 to 378) (50 specimens). The derm is thin and membranous, very small spicules are present on the ventral surface of all abdominal and thoracic segments and to a lesser degree on the dorsal surface of the last 4 abdominal segments.

Sessile pores on the venter are all of a multilocular type (Fig. 6 (20)) with 10 loculi set close to the sclerotised rim, pore diameter about 4·5 μ. The arrangement of these pores is similar to that of the quinquelocular pores in the second stage male. Smaller numbers of the same type of multilocular pore occur on the dorsum. No tubular ducts have been observed in the prepupa.

The setae of both the venter and dorsum are short and slender, arranged in regular transverse rows. The segmentation of the abdomen can be readily distinguished. At the commencement of the prepupal stage the developing gonads can readily be seen in mounted specimens examined under phase contrast. Towards the end of the prepupal stage the sperm bundles are quite prominent.

PUPAL MALE (Fig. 5 (14))

Body is elongate oval, the anal lobes are not as prominent as in the prepupa, between the lobes is a large caudal projection. The average overall length is 848 μ (range 686 to 971), the average overall

width is 262 μ (range 203 to 308) (50 specimens). Antennae, legs, and wings more developed than in the previous stage, segmentation of antennae and legs more pronounced. The derm is membranous and smooth, fine spicules are present on the venter of all abdominal segments, also meta- and meso-thoracic segments, similar spicules are present in reduced numbers on the dorsum of the last 2 abdominal segments.

Sessile pores are of the multiocular type (Fig. 6 (19)), usually with 10 loculi as in the prepupa, occasionally a pore with 6 or 7 loculi is seen (Fig. 6 (21)). The number of pores on the venter is less than in the prepupa, each abdominal segment has a pair and a small number are present on the thoracic segments. No pores were observed on the cephalic region. On the dorsum, a pair of multilocular pores occur on the penultimate abdominal segment. No tubular ducts were observed.

The body setae are similar in size and arrangement to those of the prepupa but the terminal setae of the anal lobes are longer.

TABLE 7.—*Eriococcus orariensis*—Adult Female; Length of Antennal Segments at Maturity (20 Specimens).

(Measurements in μ.)

	First	Second	Third	Fourth	Fifth	Sixth	Total
Mean	23·2	21·1	29·4	14·2	14·3	22·8	124·6
Range	18·5 to 24·5	18·5 to 23·0	26·0 to 32·0	12·5 to 17·0	12·5 to 15·5	20·0 to 24·5	118·5 to 132·5

TABLE 8.—*Eriococcus orariensis*—Adult Female; Length of Segments at Maturity (20 Specimens).

(Measurements in μ.)

	Legs					
	Anterior		Middle		Posterior	
	Mean	Range	Mean	Range	Mean	Range
Coxa	24·2	21·5 to 27·5	25·5	23·0 to 27·5	25·2	23·0 to 27·5
Trochanter-femur	66·3	60·0 to 71·0	65·8	61·5 to 71·0	67·1	58·5 to 75·5
Tibia	35·4	32·5 to 40·0	36·3	32·5 to 41·5	37·5	35·5 to 43·0
Tarsus	55·4	51·0 to 60·0	59·4	55·5 to 64·5	60·5	55·5 to 64·5
Claw	20·3	18·5 to 21·5	20·6	18·5 to 21·5	21·5	20·0 to 23·0
Overall length	201·4	191·0 to 217·0	207·5	197·0 to 217·0	211·2	194·0 to 221·5

ADULT FEMALE (Fig. 5 (6 and 7))

The average overall length of the adult female at maturity is 1169 μ (range 927 to 1430), the average overall width is 732 μ (range 560 to 900) (20 specimens).

For purposes of comparison, the length of antennal segments in the mature female is shown in Table 7, the length of the leg segments in Table 8. In the original description of *E. orariensis* no mention was made of sessile pores. In the adult female these are of the quinquelocular type (Fig. 6 (*22*)), similar to those of the intermediate female in shape and size. Pores of this type are largely confined to the venter. Occasionally multilocular pores are seen in adult females. The tubular ducts (Fig. 6 (*27*)) differ from those of all other stages, these ducts are numerous on both dorsal and ventral surfaces.

STATISTICAL EXAMINATION OF VARIABILITY IN TOTAL LEG LENGTH

The individuals selected for detailed examination came from a homogenous population established some 5 years previously by the artificial transfer of a relatively small number of individuals. At the time specimens were collected, the population was still an isolated one. Measurements were taken on insects selected as good specimens, thus representing a random sample. Variations in length of the 3 sets of legs as determined by summation of the individual segments, were examined statistically. The result of "*t*" tests on first stage nymphs is shown in Table 9. During this instar there was a significant increase in leg length in all legs. The increase in length occurred in the tarsus and trochanter-femur. Although not tested here, it is clear that at both the beginning and end of the instar the posterier leg is significantly longer than the middle leg which in turn is significantly longer than the anterior leg. Variability in length of all legs decreased during the instar, if leg length and hence size at eclosion was related to ability to survive, both an increased mean and a decrease in variability would occur during the instar without any real increase in the leg length of individual specimens.

TABLE 9.—*Eriococcus orariensis*—First Stage Nymph; Means and Results of "*t*" Tests on Total Leg Length at Eclosion, and When Fully Grown.

(Measurements in μ.)

	Legs		
	Anterior	Middle	Posterior
Eclosion	135·80 ± 0·85	141·06 ± 1·12	145·99 ± 1·19
Fully grown	140·29 ± 0·54	145·15 ± 0·75	149·00 ± 0·74
"*t*" (38 d.f.)	4·34**	3·02**	2·16*

In second stage males and females, a combined analysis of variance in leg length was done to test sex differences, individual leg differences, and differences between eclosion and the end of the stadium simultaneously. In this analysis sex differences would appear as a leg × sex interaction, sex differences in the growth of legs as a sex × stage interaction, and individual differences in leg growth as a stage × leg

interaction. There was a highly significant difference between mean leg lengths (averaged over both sexes and stages of instar). These means and their standard errors (all measurements in μ) were: anterior leg—191·48, middle leg—197·74, posterior leg—203·65, S.E. $\pm$ 0·57. There was a highly significant sex difference in the mean leg length averaged over all legs and both stages within the instar. The means were: males—215·65, females—179·59, S.E. $\pm$ 0·46. There was no significant leg $\times$ sex interaction, the observed sex difference not changing significantly from leg to leg. These means are shown in Table 10. A highly significant sex $\times$ stage interaction occurred, during the instar leg length differed significantly between the sexes (Table 11). In males the average leg length decreased significantly during the instar while leg length in the female increased significantly. There was no significant stage $\times$ leg interaction, the differences between individual legs not changing during the instar. The leg $\times$ sex $\times$ stage interaction was not significant, showing that the observed sex $\times$ stage interaction occurred consistently in all legs, these means and their S.E.'s are shown in Table 12.

TABLE 10.—*Eriococcus orariensis*—Second Stage Males and Females; Leg $\times$ Sex Means (in μ) Averaged Over Both Instar Stages.

	Legs		
	Anterior	Middle	Posterior
Male	208·75	215·68	222·53
Female	174·25	179·68	184·80

S.E. $\pm$ 0·80

TABLE 11.—*Eriococcus orariensis*—Second Stage Males and Females; Sex $\times$ Stage Leg Means (in μ) Averaged Over All Legs.

	Male	Female
Eclosion	216·86	177·33
Fully grown	214·25	181·84

S.E. $\pm$ 0·66

TABLE 12.—*Eriococcus orariensis*—Second Stage Males and Females; Leg $\times$ Sex $\times$ Stage Means (in μ).

	Eclosion		Moult	
Leg	Male	Female	Male	Female
Anterior	209·6	171·6	205·9	176·9
Middle	216·0	176·9	214·3	182·6
Posterior	224·1	183·6	221·1	186·0

S.E. $\pm$ 1·14

In the adult female, as in the first and second stages, there were significant differences in the leg means. These means were: anterior leg—201·6, middle leg—207·7, posterior leg—211·4. The Standard Error was ± 1·45 and the detectable difference at 5% level 4·08, at the 1% level 5·44.

DISCUSSION

The feasibility of using measurements for separation of the immature stages of *E. orariensis* has been demonstrated for the combined length of the tibia and tarsus. Other anatomical measurements on bulk samples have either not been sufficiently precise or the range of variation has been too great to allow their use for separation. The use of measurements for stage separation in this type of insect has a number of inherent disadvantages. Coccids have relatively few sclerotised structures and are subject to distortion in mounting. The differences in measurement in certain structures are often small enough to be masked by the variation and lack of precision in measurement. The method is time consuming and subject to operator error. For these reasons separation by measurement has been regarded only as a basis for selection of morphological characters that could be used to distinguish stages.

The use of phase contrast microscopy has enabled an examination of fine detail, such as pores and tubular ducts, to be made on unstained specimens. In the first stage nymph the presence of trilocular pores has been shown for the first time in an undoubted member of the family Eriococcidae. The bifurcated tubular ducts of the first stage may be similar to those reported by Ferris (1955) in *E. corniculatus* from China. The pores in the second stage male are, in general, of the quinquelocular type, the lateral pores on abdominal segments 3 and 4 have a variable number of loculi, between 5 and 10. Two types of tubular ducts are present in second stage males, the larger ducts having relatively broad shallow cups; there are a smaller number of minute ducts rather similar to those of the first stage nymph. Pores of the second stage female are of the usual quinquelocular type, the tubular ducts open through elongate oval or 8-shaped plates. There appear to be 2 openings to each duct. The pores of the male prepupa and pupa are of the multilocular type, the loculi being confined to a single circle. Pores and tubular ducts in the adult female are similar to those described by Ferris (1955) for the North American species of *Eriococcus*

An examination of the type and distribution of pores and tubular ducts allows ready separation of all stages of *E. orariensis*.

FIRST STAGE NYMPHS—trilocular pores, few in number; tubular ducts, few in number with bifurcated openings.

SECOND STAGE FEMALES—quinquelocular pores, few in number; tubular ducts, few in number, opening to exterior through elongate, oval, or 8-shaped plates, apparently 2 openings per duct.

SECOND STAGE MALES—quinquelocular pores relatively numerous; tubular ducts, moderate numbers, cup shallow and wide, tube to exterior short; also minute tubular ducts with bifurcated openings.

PREPUPAL AND PUPAL MALES—multilocular pores, these stages can obviously be separated on other characters.

ADULT FEMALES—quinquelocular pores, moderate numbers; tubular ducts numerous, lateral elongation of cup on one side where duct leads to gland lumen, tube to exterior longer than in second stage male.

In *E. orariensis* there are 3 stages in the female and 5 in the male. This number is similar to that reported for most coccid species in which the immature stages have been studied. Mahdihassan (1957) infers that the general pattern in female coccids is 4 stages, a careful examination of specimens of *E. orariensis* has not revealed a fourth stage in this species. It would appear that the female in some coccid species has 4 stages and in other species 3 stages.

The changes in leg length during individual stadia are interesting. It would appear that in the second stage female and first stage, these changes are associated with the trochanter-femur and the tarsus. In both cases it is probable that the apparent increase in length is associated with stretching of inter-segmental membranes and does not represent growth in the segment during a particular stadium. During the second stage in the male the shortening of the leg appears to be associated with proportionate changes in the relative width and length of the segments, this being confirmed by the fact that decreases in length occur in almost all segments between the beginning and end of the stage. The leg bud of the prepupa is relatively short and broad.

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THE HEAT PULSE METHOD FOR MEASURING RATE OF SAP FLOW IN A PLANT STEM

By R. L. Closs, Dominion Physical Laboratory, Department of Scientific and Industrial Research, Gracefield.

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Summary

The heat pulse method for measuring sap flow using two thermocouples appears to work satisfactorily for both an excised poplar twing and a growing plant. The method of measurement and the calculation of the flow are simple; they can be carried out in a few minutes. The plant is not damaged in any way by the measurement.

Introduction

A technique is presented for measuring the rate of sap flow through a plant by a heat pulse method. Basically the method consists of injecting heat into the stem of a plant and measuring the time it takes to reach a point further up the stem. Some results have been obtained by Bloodworth, Page, and Cowley (1956), who assumed that the rate of flow could be obtained simply from the consideration of the distance between the heater and the thermometer and the time taken for the temperature to reach a maximum at the point of measurement. This paper suggests that this simplified approach is not generally satisfactorily for the rates of flow characteristic of living plants.

A full theoretical approach to the problem has been made by Marshall (in press) for a line source of heat in an infinite medium. This theory has yielded satisfactory estimates for the rate of the sap flow in trees, it cannot be used for measurements on small plants.

The technique described in this paper has given satisfactory results for small plants. The theoretical approach is similar to that used by Marshall, with the modification that an approximately plane source of heat is used and the temperature is measured at two points on the stem of the plant.

Heat Flow in a Plant

The simplest mechanism envisaged for heat transfer through the stem of a plant is that the injected pulse of heat is carried along at the speed of the moving sap. When the heated sap arrives at the point of measurement the temperature passes through a maximum. The velocity of the flow is given by the equation

$$V = \frac{x}{t_m} \qquad \text{..... (1)}$$

where x is the spacing between the heater and the thermometer and t_m is the time taken for the temperature reading to reach a maximum. This is the formula used by Bloodworth, Page, and Cowley. It would be accurate if the moving sap were the sole mechanism transferring heat from the heater to the thermometer. This is not the case, although at very high rates of flow it is approximately true. When the sap is moving slowly through the stem of a plant, most of the heat is transferred away from the source by conduction and not by convection. Consequently, the value for the sap flow as given by equation (1) will be too high.

Marshall has taken account of both conduction and convection in his theory which is based on a solution of the heat flow equation (Carslaw and Jaeger, 1954).

$$\rho c \frac{\partial T}{\partial t} = K \nabla^2 T + P \qquad \text{..... (2)}$$

where c is the specific heat ρ is the density and K is the conductivity, all referred to the material through which the sap is moving. P is the quantity of heat carried by convection to the point of measurement. Its value can be shown to be given by

$$P = - a u \rho_s c_s \frac{\partial T}{\partial x}$$

where a is the fraction of any plane area perpendicular to the x axis occupied by sap streams moving with a velocity u, c_s, and ρ_s are the specific heat and the density of the sap. If this value for P is substituted in equation (2) the heat flow equation becomes

$$\frac{K}{\rho c} \Delta^2 T = \frac{\partial T}{\partial t} + a u \rho_s c_s \frac{\partial T}{\partial t} \qquad \text{..... (3)}$$

The solution for equation (3) for an instantaneous line source of heat of $Q\rho c$ calories/cm along the z axis in an infinite medium is

$$T = \frac{Q}{4\pi K t} \exp \left[- \frac{(x - Vt)^2 + y^2}{Kt} \right] \qquad \text{..... (4)}$$

where V has been written for

$$a u \frac{\rho_s c_s}{\rho c}$$

The time, t_m, when the temperature reaches a maximum, t_m, is obtained by differentiating equation (4) and equating to zero. Finally, V is extracted by taking a second point T_2, on the temperature-time curve at time t_2. Two simultaneous equations result which when solved yield for V the value

$$V = \frac{x}{t_m}\left[\frac{2{\cdot}3\log\frac{T_m}{pT_2} + \frac{p-1}{p}}{2{\cdot}3\log\frac{T_m}{pT_2} + p - 1}\right]^{\frac{1}{2}} \qquad \text{..... (5)}$$

where $p = t_2/t_m$.

This theory applies to a line source of heat perpendicular to the direction in which the sap is flowing in an infinite medium. Marshall (pers. comm.) has tested it using a long thin heater and long temperature measuring probe inserted into holes drilled through the trunk of a pine tree. This experimental arrangement approximately reproduced the conditions of the theory even though the medium was not infinite.

The particular investigation for which the heat pulse method was developed in this laboratory involved measurements on small plants. It is not possible to embed a heating wire and thermocouple in the stem of a plant and so reproduce the conditions of Marshall's theory, without considerably damaging the stem. A single turn of resistance wire wound round the stem of the plant was used as a heater and the temperature was measured on the outside of the stem 1 cm above the heater*. This arrangement of the heater produces an approximately plane source of heat perpendicular to the moving sap streams. As the heat flow takes place in one direction only, the differential equation to be satisfied by the temperature becomes

$$\frac{K}{\rho c}\frac{\partial^2 T}{\partial x^2} = \frac{\partial T}{\partial t} + au\frac{\rho_s c_s}{\rho t}\frac{\partial T}{\partial x}$$

Where the symbols have the same meaning as before.

For an instantaneous source of heat of $Q\rho c$ calories appilied at the origen of a co-ordinate system, the solution for this equation is

*It was confirmed experimentally that Marshall's theory did not apply to this experimental arrangement of the heater and thermocouple.

$$T(x,t) = \frac{Q}{\sqrt{\pi K t}} \exp\left[-\frac{(x - Vt)^2}{4Kt}\right] \quad \ldots\ldots\ldots (6)$$

This is the temperature at a point x above the heater t seconds after a pulse of heat has been applied. The temperature at a second point a distance $-x'$ below the heater is given by

$$T(-x',t) = \frac{Q}{\sqrt{\pi K t}} \exp\left[-\frac{(-x' - Vt)^2}{4Kt}\right] \quad \ldots\ldots\ldots (7)$$

At some time t_0 after the heat pulse has been applied these two temperatures will be equal. By equating the temperatures given by equations (6) and (7) at time t_0 it can be shown that

$$V = \frac{x - x'}{2t_0} \quad \ldots\ldots\ldots (8)$$

For positive values of V the lower thermocouple must be closer to the heater than the upper thermocouple.

The only measurement needed is the time that elapses between the moment when the heat pulse is applied and the moment when the temperature difference between the points x and x' returns to zero. Apart from the simplicity of the measurement and calculation the method also has the advantage that it is not necessary to know the conductivity of the material through which the sap is moving.

The relation

$$I = aV\frac{\rho_s c_s}{\rho c} \quad \ldots\ldots\ldots (9)$$

can be used to calculate the actual flow of sap through the stem of the plant. The numerical values of the density and specific heat of the sap will not be significantly different from unity. The density and specific heat of the wet wood can be calculated from the "basic density", that is the dry weight divided by the wet volume, and the

moisture content. The density is given by the relation

$$\rho = \rho_b(1 + m)$$

and the specific heat is given by the relation

$$c = \frac{(m + 0{\cdot}33)}{(1 + m)}$$

where ρ_b is the basic density, m is the ratio of water to dry matter, and 0·33 is the specific heat of cellulose. The total volume of sap flowing through the stem in unit time is given by

$$\rho_b(m + 0{\cdot}33)VA \qquad \text{..... (10)}$$

where A is the cross-section of the stem.

EXPERIMENTAL TEST OF THE THEORY

The simple experimental arrangement shown in Fig. 1, using a leafless poplar twig was set up to test the theory outlined in the previous section.

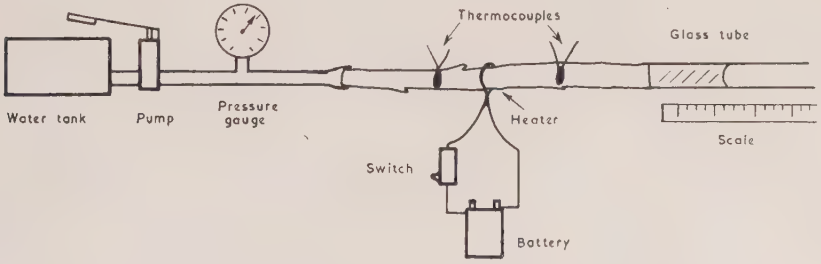

FIG. 1.—Equipment used to measure the sap flow through a poplar twig.

While a hand-operated pump maintained a constant pressure head at one end of the twig the amount of water which flowed through it was measured by observing the movement of the water along a glass tube attached to the other end. A satisfactory heat pulse was obtained by passing a current of 5 amp for 2 sec. through a single turn of 28 swg constantan wire wound round the twig. The temperature of the stem, upstream and downstream from the heater, was measured by thermocouples which were attached by adhesive tape. One thermocouple was placed 1 cm above the heater and the other thermocouple

was placed 0·5 cm below the heater. With these spacings between the heater and the thermocouples V of equation (8) is given by

$$V = \frac{900}{t_0} \text{ cm per hr}$$

if t_0 is measured in seconds.

The output from the two thermocouples, which is proportional to the temperature difference between the two points of measurement, was recorded on a moving chart instrument. The temperature difference time curves for applied pressures of 0, 40, and 80 lb/sq. in. are shown in Fig. 2.

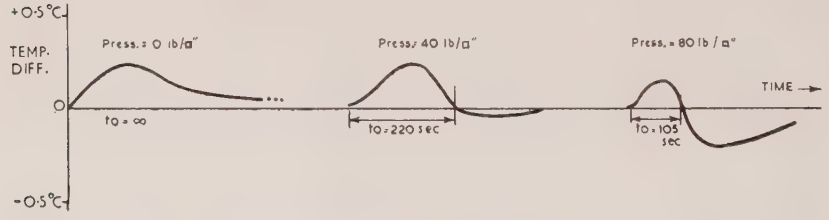

FIG. 2.—The temperature differences between two points on the poplar twig as a function of time for various applied pressures.

The calculated values for V are given in Table 1 where the results for the curves of Fig. 2 are marked with an asterisk.

TABLE 1.—Time t_0 and the corresponding calculated value of V for water forced through twig at various pressures.

Pressure (lb/sq in.)	t_0 (sec.)	V cm/hr
* 0		0
20	750	1·20
*40	220	4·1
*80	105	8·6
120	80	11·3

When the measurements were completed the bulk density and moisture content of the poplar twig were determined. Substitution of the values for the density, the moisture content, and the cross-section of

the twig in equation (10) yielded the value $0{\cdot}278\ V$ ml/hr for the volume flow of the sap. The calculated and observed volume flows are compared in Table 2 for various applied pressures.

Pressure (lb/sq in.)	V (cm/hr)	Vol. flow $= 0{\cdot}278\,V$ (ml/hr)	Vol. flow observed (ml/hr)
0	0	0	0
20	1·2	0·33	0·45
40	4·1	1·14	1·12
80	8·6	2·39	2·33
120	11·3	3·14	3·26

The agreement between the observed and the estimated rates of flow is satisfactory. The differences that do occur are probably due to errors in the measurement of the flow through the glass tube.

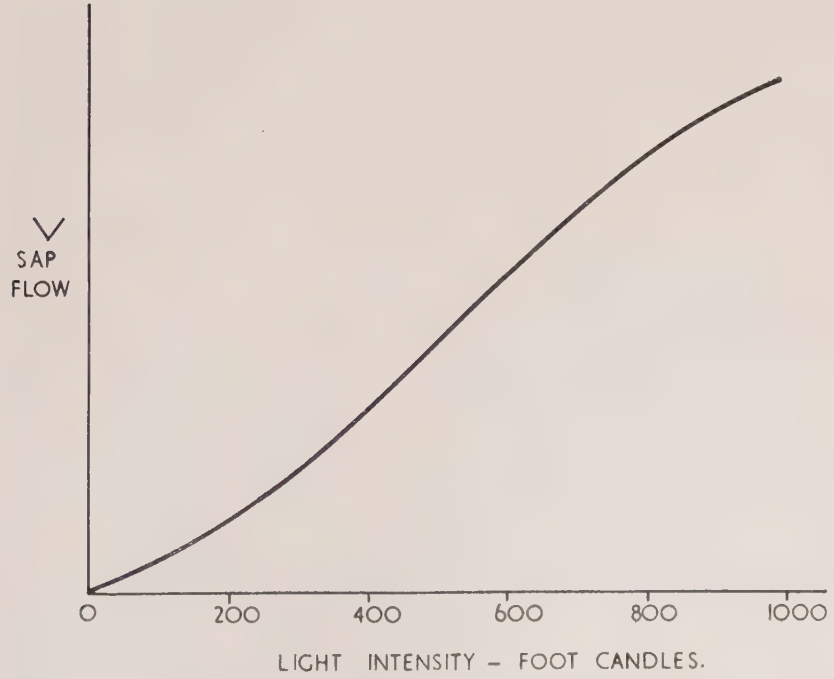

FIG. 3.—Effect of light intensity on the sap flow through the stem of a salvia plant, measured by the heat pulse technique.

Some Measurements on Plants

A species of Perennial Salvia was used for these measurements, which were carried out in a plant growth cabinet. The plant was grown in a pot of soil which was kept well watered during the experiment. The thermocouples and heater were attached to the stem of the plant about 4 cm above the level of the soil.

To demonstrate the usefulness of the method, a series of measurements of the sap flow was made at a constant temperature and humidity over a range of light intensities from zero to 1,000 foot candles. When the light intensity was changed a period of 30 minutes was allowed to elapse before the next measurement was made so that the plant could become acclimatized to its new environment. On two occasions a second measurement was made about 15 minutes after the first to check that the rate of sap flow had settled down to its new value. In both cases this was found to be so. The results are shown in Fig. 3, where the measured sap flow has been plotted against the light intensity.

The physical or physiological significance of these results will not be discussed here. They have been introduced to show that the heat pulse method for measuring sap flow works satisfactorily when it is applied to a living plant.

ACKNOWLEDGEMENT

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INCIDENCE OF COCCIDIA (SPOROZOA) IN WILD RABBITS, *Orytolagus cuniculus* (L.), IN HAWKE'S BAY, NEW ZEALAND

By P. C. Bull, Animal Ecology Section, Department of Scientific and Industrial Research, Wellington.

(Received for publication, 17 April 1958)

Summary

Some 5,000 rabbits, collected at Gwavas Forest in Hawke's Bay between 1950 and 1958, were examined for *Eimeria stiedae;* liver lesions were used as an index of infection.

Microscopic examination of bile from 960 of these rabbits showed that liver lesions are a useful index of infection in young rabbits but not in full-grown ones. The lesions heal slowly and often persist after the termination of oocyst production; in mild infections oocysts occur in the absence of macroscopic lesions.

The infection rate of *E. stiedae* was strongly influenced by the age of the host, being highest (91% in 1950-51) in animals 6 to 11 weeks old and much lower in older and in younger age groups. Vacuolated oocysts, which are common only in rabbits more than eight weeks old, are thought to indicate the onset of an acquired resistance.

The sex of the host has little, if any, influence on the infection rate.

The infection rate of *E. stiedae* in monthly samples of young rabbits remained fairly constant during the 1950-51 breeding season, but varied irregularly in the 1951-52 season. The differences found during 1951-52 are probably due to the place of collection (within the Gwavas district) rather than to the month of collection. A difference in the infection rate was found between two samples of young rabbits of uniform age collected in adjacent but ecologically different South Island localities in November, 1953.

At Gwavas, the proportion of young rabbits with severe infections of *E. stiedae* rose from 49% in 1950-51 to 60% in 1951-52 and then declined to 43% in 1953-54 and 6% in 1955-56. During this period the host population showed a marked decline in density.

In 1,029 rabbits, oocysts recovered from rectal faeces by flotation were examined microscopically; oocysts of *E. perforans* were recorded separately, but all other oocysts were grouped as *Eimeria* spp. Variations in the infection rates for *E. perforans* and for *Eimeria* spp. tended to follow those of *E. stiedae,* except that the correlation with host age was less marked.

It is suggested that the age-linked differences in the infection rate of *E. stiedae* are due mainly to acquired resistance, the locality-linked ones to environmental factors affecting the age-structure of the host population, and the long-term differences to variations in the density and age-structure of the host population.

Variations in the infection rate of *E. stiedae* in relation to host age show that this parasite is well suited as a controlling factor of rabbit populations, but there are occasions when no control is exerted because of a very low infection rate.

Introduction

This paper records some of the results obtained during one of a series of co-ordinated studies carried out by members of Animal Ecology Section on the productivity and natural mortality of the wild rabbit *Oryctolagus cuniculus* (L.) in Hawke's Bay. Other papers in the series have dealt with natural mortality and dispersal (Tyndale-Biscoe and Williams, 1955) and with reproduction (Watson, 1957). The primary purpose of these studies is to understand the factors that regulate the numbers of wild rabbits, for it is believed that such information will help to improve the efficiency of rabbit control (Wodzicki, 1950, p. 141; Bull, 1956).

It is frequently claimed that parasites are important in the natural control of animal populations and, although some such claims are advanced on insufficient evidence, others seem well founded. This aspect of host-parasite relationships has received a great deal of study overseas during recent years, and many of the more important papers have been reviewed by Lack (1954, pp. 162-191). The general conclusion emerging from this work is that host-parasite relationships vary according to the species of animals involved and the conditions under which they are living. A local study of rabbit parasites in New Zealand seemed desirable because rabbit populations are subject to marked fluctuations in density and, at least in Britain and New Zealand, some of the population declines have been associated with high populations of certain parasites (Thomas, 1883; Phillips, 1888; Gilruth, 1906; Elton, 1931; Wodzicki, 1950, p. 138).

The identity and geographic distribution of the parasites of wild rabbits in New Zealand were reported in an earlier paper (Bull, 1953). However, to assess the significance of parasites as agents of mortality it is necessary to know something about the abundance of these parasites and about the factors which control this. The present work, which is limited to the more important endoparasites, provides some of this information. It was first necessary, however, to select and test methods for recording the abundance of various parasites, and then to determine the extent to which parasite abundance might be influenced by the special characteristics of individual samples of rabbits. For instance, it is known that the infection rate of the coccidium *Eimeria stiedae* is much higher in young rabbits than in old ones (Stephens, 1952) and thus, unless the factor of host age is taken into account, the finding of a higher infection rate of *E. stiedae* in one sample of rabbits than in another might mean nothing more than the first sample contained a higher proportion of young rabbits. The results of the work will be presented in two parts, the present paper dealing with the coccidia (*Eimeria* spp.) and a subsequent paper with the helminths.

The following six species of coccidia have been recorded by Bull (1953) from wild rabbits in New Zealand: *Eimeria stiedae* (Lindemann, 1865); *E. perforans* (Leuckart, 1879); *E. piriformis* Kotlán

and Pospesch, 1934; *E. flavescens* Marotel and Guilhon, 1941*; *E. irresidua* Kessel and Jankiewicz, 1931; and, tentatively, *E. media* Kessel, 1929. During more recent work, oocysts resembling *E. magna* Pérard, 1925 and others resembling *E. exigua* Yakimoff 1934 have also been found, but these have not yet been examined in detail. The present observations refer mainly to *E. stiedae* which is a convenient species to study because it is the only one occurring in the liver, and it produces conspicuous lesions (Fig. 3) which can be used to indicate the presence and severity of infections. The remaining species occur in the intestine where mixed infections of two or more species are common, but conspicuous lesions are rare.

Apart from providing information on the kinds of host samples required for such studies, the results of the present work are of interest in relation to studies on other aspects of rabbit ecology. For instance, the data to be presented on the age-incidence of *E. stiedae* show that the parasite is well adapted as a density-dependent factor in the control of the host population; the same data allowed Tyndale-Biscoe and Williams (1955) to explain a significant rise in the survival rate in rabbits that had reached an age of 120 days. The demonstration that infection rates of *E. stiedae* at Gwavas declined consistently over a period of several years, in association with a parallel decline in the density of the host population, provides support for one of the assumptions made by Whittle (1955) in presenting his view that *E. stiedae* is an important factor in causing the periodic declines that have occurred in the rabbit population of New Zealand (Wodzicki, 1950, p. 139). The results of the present work differ from those of many comparable studies overseas in suggesting that, under the conditions experienced, the rate of infection with *E. stiedae* is controlled by the length of the host's breeding season rather than by factors affecting the survival of oocysts on the ground.

MATERIAL AND METHODS

Collection of Material

The present work is based on the examination of nearly 5,000 rabbits that were obtained between March 1950, and February 1958, from trap and poison lines located within a radius of ten miles of the Animal Ecology Field Station at Gwavas Forest, some 30 miles south-west of Napier. The animals were collected at the rate of approximately 150 every 28 days from March 1950 to March 1952, and at irregular intervals thereafter.

*According to Becker (1956) *E. flavescens* Marotel and Guilhon, 1941 is a "synonym of *E. media* ?", but the name *E. flavescens* is retained in the present work because the oocysts examined had no extra-residual body and thus resembled the figure of *E. flavescens* in Marotel and Guilhon (1941) rather than that of *E. media* in Becker (1934).

The trap and poison lines were laid according to the needs of the control policy, and rabbits for dissection had to be obtained from wherever they were available within the general area. As a result, all the rabbits came from areas of high or medium density, and it was not possible to get successive monthly samples from exactly the same locality.

The main material, consisting of 4,143 rabbits collected during 1950-52, provided information on the extent to which the infection rate of *E. stiedae* was affected by the sex ratio and age structure of the host sample, by the month of collection, and by minor variations in the locality of collection. To obtain further data on yearly variations in the infection rate, 679 rabbits were collected at Gwavas during subsequent years, 241 rabbits between November 1953 and January 1954, 252 between December 1955 and February 1956, 80 in February 1957, and 106 in February 1958. Finally, two large samples were obtained from districts other than Gwavas, 375 rabbits from Duntroon near Oamaru in November 1953, and 164 from Reporoa in the Rotorua-Taupo district in December 1953. Most of the rabbits listed above were also examined for helminths, and they were included among the rabbits used by Watson (1957) for his study of reproduction.

FIG. 1.—Unplanted portion of Gwavas Forest (foreground) typical of higher country from which rabbits were obtained. (*Photo R. L. Edgar.*)

Features of the Collecting Area

The collecting area comprises a central block of rolling to fairly steep country, varying in altitude from 800 ft to 1,700 ft above sea-level, surrounded by extensive areas of relatively flat land. The mean annual rainfall at Forest Headquarters is 48 in., and mean monthly

temperatures range from 43° F in July to 62° F in January. The soils (Mangatahi and Gwavas sandy loams) are light, with fairly rapid drainage and low natural fertility; pasture growth in spring is early and pastures dry off rapidly in dry weather (Pohlen, *et al.*, 1947, p. 90).

Following the removal of the original native vegetation, the area was converted to pasture and grazed by sheep, but subsequently much of the higher country reverted to manuka (*Leptospermum scoparium*) scrub, and in 1947 this area was acquired by the New Zealand Forest Service. Much of the forestry area is now planted in pines, but on the unplanted portion many of the ridges have open areas of grass (Fig. 1) bordered by stands of manuka which extend down into the steep-sided stream beds. The surrounding farmland includes considerable areas of high quality pastures of introduced grasses and clovers. In the wide river beds of the flatter country (Fig. 2), thickets of gorse (*Ulex europaeus*) and blackberry (*Rubus fruticosus*) provide good cover for rabbits which come out to feed on the adjacent pastures.

The rabbit population increased greatly during the middle nineteen-forties and reached peak numbers about 1948-49. Since then, a vigorous control programme has been in operation and the number of rabbits has gradually declined through this and other causes (Bull, 1956). Today, the former heavy population has been reduced to a very light one with occasional pockets of medium density. The rabbits use the scrub for shelter and, apart from a few small warrens in open areas, dig burrows only for breeding purposes.

FIG. 2.—Part of Gwavas Station typical of lower (farm-land) country from which samples of rabbits were obtained. (*Photo R. L. Edgar.*)

Examination of Material

In the field, each rabbit was weighed and sexed. The animal was then cut open and the alimentary tract, liver, and embryos (if any) removed, and the animal weighed again to obtain the paunched weight. The liver was examined for the presence of lesions caused by *E. stiedae*, the extent of such lesions being assessed according to the following scale:

0 negative	(no lesions found)
1 light	(one or two spots present)
2 medium	(up to one half of the liver affected by lesions)
3 heavy	(more than half the liver affected by lesions (Fig. 3))

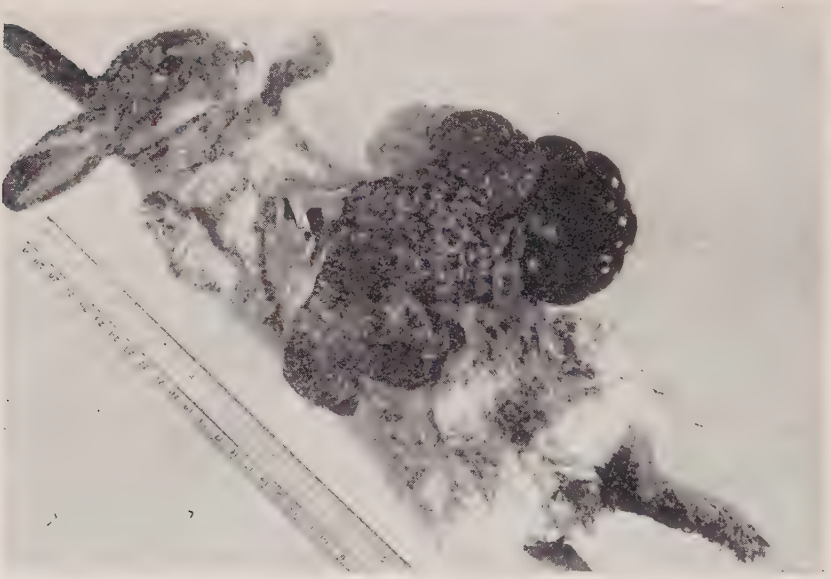

FIG. 3.—Grade 3 lesions in liver of young rabbit infected with *E. stiedae*. (*Photo S. N. Beatus.*)

The gall bladder and a piece of the rectum were removed from approximately half the rabbits in each of the monthly samples collected between March 1950, and March 1951 inclusive. This material was preserved in formalin for later examination.

In the laboratory, smears were made from the contents of the preserved gall bladders, and these were examined microscopically, the abundance of oocysts being recorded as follows:

0 negative	(no oocysts found)
1 light	(less than one oocyst per mean, low-power microscope field)
2 medium	(1 to 5 oocysts per field)
3 heavy	(over five oocysts per field)

The number of oocysts in heavy infections (sometimes over 100 per microscope field) was usually so much greater than in light ones (often only 2 or 3 oocysts in the whole preparation) that the deficiencies of the examination technique were unimportant for the differentiation of light and heavy infections.

The incidence of the intestinal species of *Eimeria* was studied in the preserved rectal faeces of 1,029 rabbits. The oocysts were recovered from the faeces by flotation in zinc sulphate solution using approximately one gram of faecal matter from each rabbit; the abundance of the oocysts was recorded by reference to the scale employed for *E. stiedae* in the bile. It was not possible to identify all the oocysts recovered from rectal faeces because the material had been preserved before sporulation could occur, and because the large number of animals to be examined precluded measuring more than a few oocysts. However, the oocysts of *E. perforans* could be identified at once by their small size, symmetrical shape, and lack of an operculum. Two groups were therefore recognized, namely—

(a) small, non-operculate oocysts (*E. perforans* and perhaps a few *E. exigua*), and

(b) larger, operculate oocysts (the remaining intestinal species and *E. stiedae*).

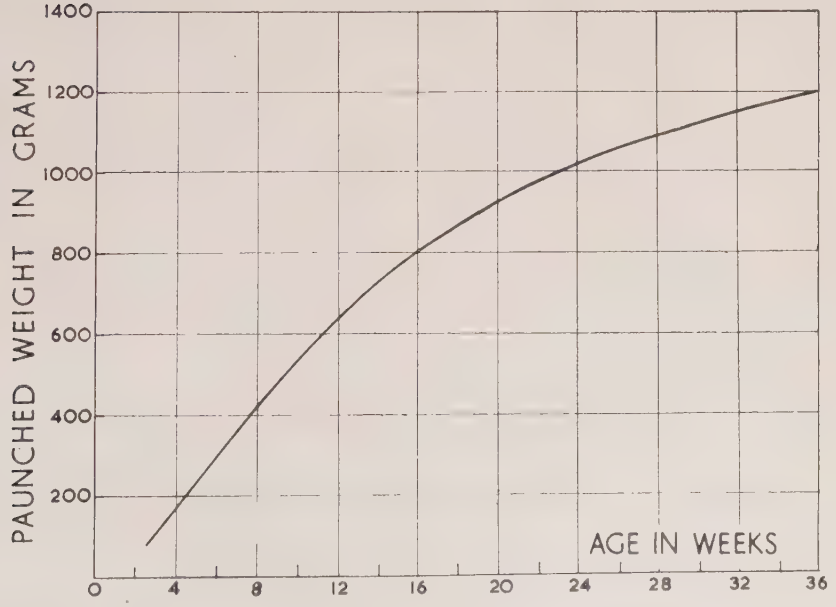

FIG. 4.—Relationship between paunched weight and age of rabbits. (From Whittle, 1955.)

Analysis of Data

The data were transferred to Powers-Samas punch cards, and the Applied Mathematics Laboratory, D.S.I.R. sorted the cards and provided tables to show variations in the infection rate according to the age and sex of the host and the place and time of collection.

Paunched weight was used to indicate host age, since there is normally a close correlation between age and weight in young rabbits (Southern, 1940; Tyndale-Biscoe and Williams, 1955; R. H. Taylor, pers. comm.). Tyndale-Biscoe and Williams (1955) found that the growth rate of marked rabbits in a wild population was similar to that of captive wild rabbits, even though *E. stiedae* was prevalent in the wild population but rare or absent in the captive animals. This suggests that any distortion caused by coccidiosis to the normal age-weight relationship is relatively small. It is considered, therefore, that for the purposes of the present study, paunched weight provides an adequate index of age in young rabbits. In full-grown animals weight is much less reliable as a criterion of age (Watson and Tyndale-Biscoe, 1953; Tyndale-Biscoe and Williams, 1955), but, in the absence of other criteria, weight can still be used to divide a sample of rabbits into broad groups of increasing mean age. All weights mentioned in the present paper are paunched weights; the advantages of using paunched weight rather than dead weight have been summarized by Watson and Williams (1955), and Fig. 4, taken from Whittle (1955), provides a convenient means of correlating paunched weight with age. The age of full-grown rabbits can now be assessed from the degree of ossification of the tibiae (Watson and Tyndale-Biscoe, 1953) and of the lumbar vertebrae (R. H. Taylor, pers. comm.) but this information was not available when the present study was begun.

To examine seasonal differences in the infection rate, 28-day periods were used in preference to calendar months. The 13 collecting periods in each year were as follows:

(1) 1 January to 28 January
(2) 29 January to 25 February
(3) 26 February to 25 March
(4) 26 March to 22 April
(5) 23 April to 20 May
(6) 21 May to 17 June
(7) 18 June to 15 July
(8) 16 July to 12 August
(9) 13 August to 9 September
(10) 10 September to 7 October
(11) 8 October to 4 November
(12) 5 November to 2 December
(13) 3 December to 31 December

In analysing the present material, it was usually found convenient to sum infections of grades 2 and 3, and the value thus obtained is referred to as substantial infections. The use of this value discounts any errors made in separating very light infections from negative ones, and only substantial infections are likely to be significant in causing mortality in the host population. The term "infection rate" as used in this paper means the percentage of rabbits infected. If infections of a certain grade are being considered, this fact is indicated in parentheses, e.g., "infection rate (grades $2 + 3$)."

The results of the work are presented below in seven sections, the first six dealing with various aspects of *E. stiedae* and the seventh with the more limited data on the intestinal species. Each section provides a basis for assessing the significance of data in subsequent sections. For this reason it has been necessary to discuss each set of data before presenting the next set. A final section of discussion deals with the more general implications of the work as a whole.

RESULTS AND INTERPRETATION

(1) *Validity of the Field Examinations*

The severity of *E. stiedae* infections in 960 rabbits was assessed both macroscopically (liver lesions) and microscopically (number of oocysts), and Table 1 shows the extent of agreement between the two methods; young (under 1,000g) and full-grown rabbits are grouped separately. The scale for recording lesions is not directly related to that for oocysts so exact agreement between the various grades of positive infection should not be expected. However, if liver lesions provided a perfect index of *E. stiedae* infection, oocysts could be expected in the bile of all the rabbits that had liver lesions and in none of those that did not. This expectation is not fully realized.

TABLE 1.—Comparison of Results of Macroscopic and Microscopic Examinations for *E. stiedae*.

Rabbits < 1,000g

Lesions Scale of Infection	Oocysts Scale of Infection 0	1	2	3	Total Rabbits
0	74	41	8	7	130
1	15	24	7	24	70
2	6	7	10	39	62
3	2	6	6	47	61
Total Rabbits	97	78	31	117	323

Rabbits ≥ 1,000g

Lesions Scale of Infection	Oocysts Scale of Infection 0	1	2	3	Total Rabbits
0	376	91	7	8	482
1	87	20	7	5	119
2	15	3	4	2	24
3	4	4	1	3	12
Total Rabbits	482	118	19	18	637

Table 1 shows that of 193 young rabbits with lesions, 23 (12%) had no oocysts, and that of 226 with oocysts 56 (25%) had no lesions. These discrepancies can be explained if severe lesions tend to persist after the termination of oocyst production and if very mild infections produce no conspicuous lesions. There is evidence that both

these conditions are quite common. Of the 23 rabbits with liver lesions but no oocysts, 21 weighed more than 700g and were thus beyond the age of heaviest *E. stiedae* infection (Fig. 5) and are likely to have been in process of recovery; of the 56 rabbits with oocysts but no lesions, 41 had very few oocysts (i.e., mild infections).

Thus, when liver lesions are used to assess the infection rate of *E. stiedae* in young rabbits, a small proportion of the animals that have almost recovered will be classed as positive and a considerably greater proportion of the animals with very light infections as negative. Results are thus likely to indicate an unduly low infection rate. The present work is concerned mainly with substantial infections, so the failure to detect a proportion of the light infections is not important. Similarly, since lesions in the absence of oocysts indicate a substantial infection in the recent past, the general picture is not distorted if a few such animals are included in the count of those that still have active infections.

It is considered, therefore, that liver lesions provide a valid index of the prevalence of substantial infections of *E. stiedae* in young rabbits. This is further supported by data presented in subsequent sections where it is shown that whichever method is used to assess infection, the relation between the infection rate of the parasite and such factors as the age-structure of the host sample or the time or place at which the sample was collected remains the same. In view of these considerations, and because a much greater number of rabbits could be examined in a given time, the macroscopic method was adopted in preference to the microscopic one.

With full-grown rabbits, the discrepancies between the results obtained by the two methods are very much greater. Of 155 adults with lesions, 106 (68%) had no oocysts in the bile, and the same proportion of those with oocysts had no lesions (Table 1). The causes of these discrepancies are probably the same as those which operate, but to a much lesser extent, in young rabbits; namely, absence of lesions in mild infections and, in heavier infections, the persistance of lesions after the termination of oocyst production. Table 1 shows that adult rabbits that are positive for oocysts of *E. stiedae* have a much higher proportion of light infections (76%) than do young rabbits (35%); a greater proportion of animals with oocysts but no lesions is therefore to be expected in the former group. A greater proportion of recovery stages (lesions but no oocysts) is also to be expected in full-grown rabbits because some young animals with active infections have relatively little time to complete their recovery before they reach a paunched weight of 1,000g and pass into the adult age group (Table 3). The occurrence of 15 full-grown rabbits having substantial numbers of oocysts but no lesions (Table 1) can be explained by the fact that non-viable oocysts sometimes become clumped together in the gall bladder (Bull, 1953) where they are likely to remain long after all other signs of a former infection have been lost.

Liver lesions in full-grown rabbits may give some indication of the prevalence of substantial infections of *E. stiedae* during an earlier period, but if the proportion of active infections in a sample is required, microscopic examination must be used. However, this limitation in the method is of no great consequence because, in studies of the present type, interest is directed mainly to the high-infection age group (young rabbits), and it has been shown that the technique is quite valid for use with this group.

(2) *Infection Rate in Relation to Age of Host*

It was shown in the preceding section that liver lesions are sometimes found in the absence of oocysts, and vice-versa. Further, it was reported in earlier work (Bull, 1953) that oocysts in full-grown rabbits are often vacuolated and non-viable. Oocysts of this type were frequently noted during the present study and were recorded separately. The infection rate can be assessed therefore on three criteria, namely, lesions, total oocysts, and viable oocysts.

These three criteria have been used in Fig. 5 which correlates the infection rate (grades 2 + 3) at Gwavas in 1950-51 with the weight (age) of the host. The similarity in the shape of the three curves indicates that, irrespective of the criterion used, the infection rate is strongly correlated with host age, being highest (up to 91%) in rabbits of 300g to 600g (6 to 11 weeks old) and much lower in both younger and older animals; the infection rate (grades 2 + 3) in rabbits weighing more than 1,000g (more than 22 weeks old) is invariably less than 10%. This marked influence of host age on the infection rate of *E. stiedae* makes it important to standardize the factor of age before looking for differences between infection rates

TABLE 2.—Incidence of Oocysts in Full-grown Rabbits of Different Ages

Approximate Age of Rabbits	Scale of *E. stiedae* Infection				Total No. Rabbits
	0	1	2	3	
6 to 10 months	14	26	7	3	50
10 months to about 2¼ years	25	1	—	—	26
2¼ years to nearly 3 years	14	2	—	—	16
3 years and over	14	—	—	—	14
All rabbits	67	29	7	3	106

in samples of rabbits collected at different times or different places. It was therefore considered desirable to confine such analyses to rabbits weighing from 300g to 800g inclusive. Rabbits of this age group (6 to 16 weeks) have a high infection rate, and the group can provide adequate numbers of animals for collection during the summer months, and also accommodates any minor irregularities in the age-weight relationship.

TABLE 3.—Prevalence of Lesions of *E. stiedae* at Gwavas, 1950-52.

Year	1950-51										1951-52									
Sex of Rabbits	Males					Females					Males					Females				
Scale of Infection	0	1	2	3	T*	0	1	2	3	T*	0	1	2	3	T*	0	1	2	3	T*
Host weight (g)																				
100	15	—	—	1	16	12	1	—	1	14	8	1	1	—	10	10	1	—	1	12
200	32	1	2	5	40	36	2	—	3	41	41	5	—	2	48	41	3	—	1	45
300	26	8	10	20	64	11	5	9	18	43	9	3	4	13	29	9	4	5	19	37
400	8	10	13	18	49	4	7	11	10	32	3	1	1	14	19	—	2	3	11	16
500	6	6	20	7	39	4	4	21	13	42	2	4	8	12	26	3	4	10	16	33
600	8	9	11	6	34	5	9	10	10	34	5	7	6	17	35	5	2	11	9	27
700	12	18	4	3	37	8	11	9	4	32	9	6	9	9	33	5	18	11	8	42
800	26	14	6	5	51	16	22	6	5	49	5	18	5	4	32	10	19	10	11	50
900	43	23	2	3	71	36	16	5	3	60	26	23	9	7	65	15	32	9	11	67
1,000	85	21	4	3	113	63	22	6	—	91	41	35	10	6	92	50	36	3	9	98
1,100	109	42	8	1	160	64	19	5	2	90	107	47	10	4	168	84	45	3	—	132
1,200	137	24	6	1	168	89	28	8	2	127	129	49	5	1	184	118	55	4	2	179
1,300	112	16	5	1	134	87	20	5	1	113	139	53	6	—	198	120	47	4	1	172
1,400	89	13	3	1	106	83	23	2	—	108	143	38	1	1	183	110	38	3	2	153
Total Rabbits	708	205	94	75	1082	518	189	97	72	876	667	290	75	90	1122	580	306	76	101	1063

*T = Total of rabbits in each Group

TABLE 4.—Prevalence of Oocysts of *E. stiedae*, Gwavas 1950-51.

	TOTAL OOCYSTS										VIABLE OOCYSTS				
	Male Rabbits					Female Rabbits					Both Sexes				
Scale of Infection	0	1	2	3	Total	0	1	2	3	Total	0	1	2	3	Total
Host weight (g)															
100	4	—	—	2	6	4	2	—	—	6	8	2	—	2	12
200	8	1	—	5	14	7	1	—	3	11	16	1	—	8	25
300	7	—	1	12	20	3	1	1	11	16	11	1	2	22	36
400	1	2	1	16	20	—	—	1	14	15	2	2	2	29	35
500	—	—	1	9	10	1	5	—	14	20	6	2	1	21	30
600	—	6	4	9	19	—	3	3	5	11	13	4	3	10	30
700	2	3	3	8	16	4	6	3	8	21	20	3	2	12	37
800	9	18	1	4	32	9	8	6	2	25	47	5	3	2	57
900	26	15	2	1	44	21	11	4	—	36	66	12	1	1	80
1,000	53	12	3	1	69	31	17	3	3	54	121	1	—	1	123
1,100	74	19	4	2	99	38	15	1	1	55	149	5	—	—	154
1,200	81	16	1	2	100	53	11	4	3	71	170	1	—	—	171
1,300	71	11	—	—	82	39	5	—	1	45	124	3	—	—	127
1,400+	44	5	—	—	49	31	7	—	2	40	87	2	—	—	89
Total	380	108	21	71	580	241	92	26	67	426	840	44	14	108	1006

Apart from its main purpose of showing the importance of standardizing host age before seeking differences in infection rates, Fig. 5 and its supporting data (Tables 2, 3, and 4) throw light on certain aspects of the epidemiology of *E. stiedae*. The shape of the age-incidence curve (Fig. 5) can be explained on the basis of acquired resistance, and in this connection the high rates of infection found in young rabbits at Gwavas in 1950-51 (Fig. 5) are of particular interest. Young rabbits begin to to emerge from their burrows when they are some 3 weeks old (Southern, 1940) and have a paunched weight of about 150g (Fig. 4). Many animals become infected with *E. stiedae* during the following few weeks and by the time they are 8 weeks old a very high proportion is infected. Fig. 5 shows the prevalence of substantial infections, but if light infections are also included, the infection rate for oocysts reaches the surprisingly high figure of 97% in the 400g and 500g weight groups (Table 4). Judging by the prevalence of lesions, infection rates at Gwavas were even higher in the following year (1951-52). It is clear, therefore, that during the period 1950-52, virtually all young rabbits at Gwavas had experienced infection with *E. stiedae* by the time they were 10 weeks old.

The declining infection rate in rabbits more than 11 weeks old (600g in Fig. 5) is due to the recovery of some animals and to the death of others, thus leaving only animals with milder infections to appear in the samples. The proportion of animals that die is unknown,

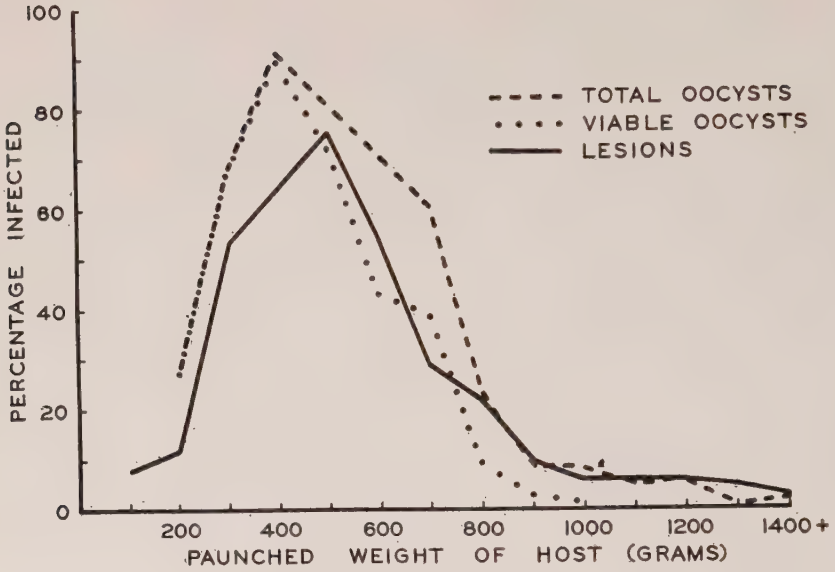

FIG. 5.—Relationship between infection rate (grades 2 + 3) of *E. stiedae* and paunched weight (age) of host, Gwavas 1950-51.

but there is circumstantial evidence that, when the infection rate (grades 2 + 3) is high, the mortality rate may be considerable (Tyndale-Biscoe and Williams, 1955). It is evident from Fig. 5 that this mortality will occur mainly in animals which are 6 to 14 weeks old (300g to 700g), since these are the ones having a high rate of substantial infections.

The presence of vacuolated oocysts affords evidence of recovery from infection. The rate of infection with vacuolated oocysts is represented in Fig. 5 by the difference between the curves for viable oocysts and for total oocysts. This difference is negligible in rabbits weighing 400g or less, but thereafter vacuolated oocysts become more frequent and, in full-grown rabbits, almost all infections show oocysts of this type. It is interesting that the occurrence of non-viable oocysts should be virtually confined to rabbits weighing more than 400g, for in such animals the infection rate for both lesions and oocysts declines progressively with increase in host weight. The appearance of vacuolated oocysts in the age group showing a declining infection rate suggests that rabbits yielding such oocysts are recovering. This view is supported by the results of experimental work on the coccidia of kangaroo rats (*Dipodomys*) which showed that the onset of immunity is indicated by the production of degenerate oocysts (Doran, 1953).

Active infections of *E. stiedae* are extremely rare in adult rabbits even though such animals, particularly breeding females, often graze on areas frequented by heavily infected young rabbits. The absence

of infection in adult rabbits, despite the opportunity to acquire it, suggests that these animals have developed some resistance to the parasite by virtue of previous infection or of physiological changes associated with increased age. The matter is examined further in the general discussion that concludes this paper.

More detailed information on the age incidence of *E. stiedae* in full-grown rabbits was obtained by the microscopic examination of bile from 106 rabbits collected near Gwavas in February 1958 (Table 2). The animals were divided into four groups of increasing age according to the degree of ossification of the tibiae and lumbar vertebrae (R. H. Taylor, pers. comm.). The exact limits of the three older age classes are the subject of current research, and the values supplied in the first column of the table are therefore provisional. The table shows that, even though the infection rate is low in full-grown rabbits, host age still exerts an important influence on the prevalence of *E. stiedae*. Substantial infections are confined to rabbits less than 10 months old, and even light infections are rare in older animals. Most of the oocysts recovered were vacuolated and non-viable; 11 rabbits had one or more oocysts of normal appearance, but these animals were all in the youngest age group. It seems, therefore, that the presence of oocysts in full-grown rabbits usually indicates incomplete recovery from a juvenile infection rather than a new infection acquired in adult life.

Liver lesions also are more frequent in young full-grown rabbits than in older animals. Data collected at Gwavas during 1951-52 showed that the infection rate with substantial lesions in 683 full-grown rabbits under 10 months old (8%) was significantly higher than the 2% found in 782 older animals ($P < 0{\cdot}01$). This lower infection rate in older rabbits confirms that lesions do disappear with time, and shows that, if any old rabbits develop new lesions, the number of such animals is less than the number loosing the last signs of juvenile infections.

(3) *Infection Rate in Relation to Sex of Host*

From data in Table 3, it can be shown that in 1950-51, the infection rate for substantial liver lesions in young rabbits was higher in females than in males, but this trend was apparent only in animals weighing less than 1,000g. In 506 rabbits weighing from 300g to 800g inclusive, the infection rate was 54% in females but only 45% in males. This difference just reaches statistical significance ($P = 0{\cdot}02 - 0{\cdot}05$) and, furthermore, the trend is consistent even if the sample is divided into sub-groups according to host weight or period of collection. However, there are reasons for suspecting that the difference is spurious.

Data based on microscopic examination of bile from 225 of these rabbits (Table 4) suggest a slightly higher infection rate in females (63% in females and 59% in males), but the difference is less than might be expected to occur from chance ($P = 0{\cdot}70$) and in the 500g and 700g weight groups, the infection rate is higher in males than in females. Similarly, in 1951-52 the infection rate with substantial liver lesions in 379 rabbits of 300g to 800g (Table 3) is only 1% higher in females

than in males ($P = 0{\cdot}80$). Further, there is no evidence of a bias towards heavier infections among females in the smaller samples of young rabbits collected in different localities during 1953, namely: Reporoa, 102 rabbits (infection rate for substantial lesions 1% lower in females); Gwavas, 68 rabbits (13% lower in females); grassy paddock near Duntroon, 64 rabbits (1% higher in females); and riverbed near Duntroon, 77 rabbits (2% lower in females). Finally, the figures supplied by Stephens (1952) for 473 young rabbits collected in Wales suggest that any bias that may occur is towards a higher infection rate in males.

In view of these considerations, the apparently higher infection rate (grades $2 + 3$ lesions) among young females at Gwavas in 1950-51 must be regarded with suspicion. All likely causes of bias have been examined but no convincing explanation has been found and the reason for the higher infection rate in females remains unknown. However, even in 1950-51 the bias was relatively slight (9%) and its statistical significance is only apparent because of the large number of rabbits examined. Clearly therefore, if sex of host has any effect on the infection rate of *E. stiedae,* it is small and may be disregarded in subsequent analyses of the present material.

FIG. 6.—Open riverbed near Duntroon providing rabbits with a low infection rate of *E. stiedae.* (*Photo J. S. Watson.*)

(4) *Infection Rate in Relation to Locality of Collection*

The Gwavas material was usually collected at a slightly different locality each month, and differences in the infection rate of *E. stiedae*

due to the place of collection can therefore rarely be separated from those due to the time of collection. Before considering the meagre data available from Gwavas, it may be useful to consider first a good example of a locality difference which was detected in some material from the South Island.

In November 1953, rabbits were collected from two localities about two miles apart in the Duntroon district, some 20 miles north-west of Oamaru in North Otago. The first locality was a dry, over-grazed riverbed (Fig. 6) and the second a flat paddock of fairly long grass (Fig. 7). Of 77 rabbits weighing from 300g to 800g collected on the riverbed, only 16 (21%) had substantial liver lesions, while from the paddock of grass 42 out of 64 animals (66%) had infections of this kind; the difference between the infection rates is significant ($P < 0{\cdot}01$). This result was confirmed by examining the preserved gall bladders from some of the rabbits, 31 from the riverbed and 26 from the paddock of grass. The former sample contained 10 animals (32%) with substantial oocyst infections and the latter 16 (62%), and the difference, even in the small samples available, just reaches statistical significance ($P = 0{\cdot}05$).

FIG. 7.—Grassy paddock near Duntroon providing rabbits with a high infection rate of *E. stiedae*. (*Photo J. S. Watson.*)

The sex ratio of the rabbits was similar in the two samples, the factor of host age was standardized, and the examination procedure was such as to minimise any human bias. It seems, therefore, that the

difference between the infection rates is real. The moister microclimate under the long grass (Crofton, 1948) might allow better survival of oocysts since these are known to be susceptible to desiccation (Landers, 1953). However, apart from differences in vegetation, there were differences in the breeding rates of the rabbits on the two areas, those on the paddock of grass having started breeding successfully at a much earlier date and, in November, showing a higher pregnancy rate and larger litter size (Watson, 1957). It is likely, therefore, that young rabbits had been present on the paddock of grass for a longer period than on the dry riverbed and these animals, being susceptible to *E. stiedae* infection, would increase the rate of oocyst deposition. Thus, both oocyst survival and oocyst production were probably higher on the paddock of grass and, since the severity of coccidiosis is known to be proportional to the number of oocysts ingested (Becker, 1934, p. 81; Lund, 1949; Brackett and Bliznick, 1952), a higher rate of substantial infections was to be expected in this situation.

Although there were ecological differences between the various collecting localities at Gwavas—and sometimes even within a single collecting locality—such differences were much less extreme than those described above for Duntroon. In January, 1952, rabbits were collected from two rather similar and adjacent localities at Gwavas and the proportion of substantial infections of *E. stiedae* in samples of 50 and 35 young rabbits (300g to 800g) was respectively 74% and 51%, but this difference is not significant ($P = 0{\cdot}06$). Similarly, the infection rate did not vary significantly in seven samples of young rabbits collected at various Gwavas localities between September 1950, and March 1951 (Fig. 8). On the other hand, significant differences in the rate of infection were found in five samples collected between October 1951, and February 1952. These differences are discussed in the following section, where it is concluded that they were probably caused by a locality effect rather than a seasonal one.

Although the hypothesis remains unproved, it seem that within the Gwavas area, there are locality differences which may occasionally have an effect on the infection rate of *E. stiedae*. However, the few possible instances of such an effect refer to differences which are of small magnitude (Fig. 8) compared to those due to host age (Fig. 5) and year of collection (Fig. 9). It is concluded, therefore, that although locality differences in the infection rate of *E. stiedae* at Gwavas cannot be ignored, their influence is of minor importance.

(5) *Infection Rate in Relation to Month of Collection*

In the upper part of Fig. 8, the infection rate (grades $2 + 3$) with liver lesions in rabbits of 300g to 800g is shown in relation to the period of collection. Data are available for three different years, but the period covered varies somewhat from year to year—depending on the availability of sufficient rabbits of the required weight (Table 5). In 1950-51, the infection rate varied from 56% in September,

December, and February to 38% in March, but none of the differences is significant ($P > 0{\cdot}01$ in each instance). In 1951-52, on the other hand, the infection rate varied widely and often significantly from month to month, namely, a decrease from October to November ($P = 0{\cdot}04$), an increase from November to December ($P < 0{\cdot}01$), a decrease from December to January ($P < 0{\cdot}01$) and an increase from January to February ($P = 0{\cdot}07$). These variations alternate in direction and show no consistent trend of either increase or decrease over the season as a whole. In 1953-54, however, there was a significant decline in the infection rate from October through to January.

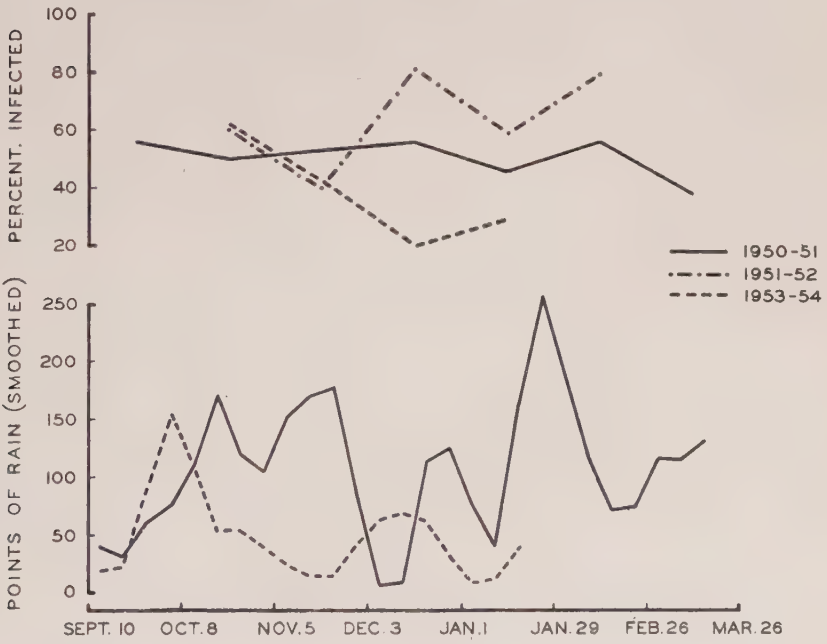

FIG. 8—UPPER: Seasonal varitions in the infection rate (grades 2 + 3) of *E. stiedae* lesions in young (300g to 800g) rabbits at Gwavas.
LOWER: Weekly rainfall (smoothed).

It seemed that rainfall might provide some explanation for these results because rainfall is itself a somewhat variable quantity and moist conditions have been reported overseas as favouring a high infection rate of coccidiosis in hares (Boughton, 1932; Naumov, 1939). The two lower lines in Fig. 8 show the weekly rainfall (smoothed) at Gwavas during the appropriate months of 1950-51 and 1953-54. The figures for 1951-52 were intermediate and have been omitted from the graph in the interests of clarity. In 1950-51, with a highly variable rainfall, the infection rate for liver lesions remained fairly

constant throughout the period. In 1951-52, with slightly lower rainfall figures but a similar distribution of rain, the infection rate of *E. stiedae* was highly variable and generally higher than in the previous year. The variations in the infection rate of the parasite showed no obvious correlation with rainfall, and they are probably due to differences between the localities from which the monthly samples of rabbits were obtained. In 1953-54, on the other hand, there appeared to be a direct relationship between rainfall and infection rate because, with a low rainfall during most of the period, the rate of infection with *E. stiedae* fell to a relatively low level (Fig. 8). However, this relationship may be fortuitous because there is no evidence of its existence in material collected in subsequent years. The total rainfall recorded at Gwavas for the period September to December inclusive was 9·20 inches in 1953 and 10·28 inches in 1955; yet the infection rate of *E. stiedae* was very much lower at the end of the latter year (Fig. 9); these rainfall figures are only slightly below the 11·23 inches recorded in the corresponding months of 1951, which was a year of unusually high infection with *E. stiedae*. It is evident, therefore, that within the range of weather conditions experienced at Gwavas, there is no correlation between the infection rate of *E. stiedae* and the amount of rain. Since grass and other vegetation provides a moist microclimate at ground level (Crofton, 1948), it is likely that at Gwavas many oocysts will fail to experience the effects of periods of low rainfall, provided these periods are not too long.

It is interesting that the rate of infection is no higher at the end of the breeding season than at the beginning (Fig. 8). There must be considerable seasonal variation in the rate of oocyst deposition because viable oocysts are produced in quantity only by rabbits weighing less than 1,000g (Fig. 5), and there are few such animals in the population during the winter months. It might be expected, therefore, that rabbits born early in the breeding season would be exposed to smaller doses of oocysts than those born later. However, it is apparent from Fig. 8 that substantial numbers of oocysts must be available even at the beginning of the breeding season. Although oocysts are produced by the small number of young rabbits born outside the main breeding season, this source of oocysts seems inadequate to explain the high infection rate early in the season, and it seems likely that considerable numbers of oocysts remain viable on the ground from one breeding season to another.

Although rabbits in the 900g to 1,200g weight group are available at all seasons of the year (Table 5), such animals are of little value in showing seasonal differences in the infection rate of *E. stiedae*, because the parasite has a low rate of infection in such animals and it is difficult to eliminate the effect of differences in host age (Fig. 11).

(6) *Infection Rate in Relation to Year of Collection*

Fig. 9 illustrates the relationship between host weight and the infection rate (grades 2 + 3 lesions) of *E. stiedae* in four different years.

TABLE 5.—Seasonal Variations in Prevalence of Lesions of *E. stiedae*, Gwavas, 1950-52.

Weight of Rabbits		< 300g					300 to 800g					900 to 1,200g					≥ 1,300g				
Scale of Infection		0	1	2	3	T*	0	1	2	3	T*	0	1	2	3	T*	0	1	2	3	T*
Year	Period																				
1950	3	—	—	—	—	—	13	6	1	—	20	55	13	3	2	73	23	1	1	—	25
1950	4	—	—	—	—	—	3	—	—	—	3	53	18	11	2	84	25	8	3	—	36
1950	5	—	—	—	—	—	—	1	—	—	1	73	21	4	2	100	46	6	3	—	55
1950	6	—	—	—	—	—	—	—	—	—	—	40	9	2	1	52	68	17	5	—	90
1950	7	—	—	—	—	—	2	1	—	—	3	67	12	6	—	85	35	3	—	—	38
1950	8	1	—	—	—	1	3	1	—	—	4	59	8	2	2	71	58	2	—	—	60
1950	9	5	—	—	—	5	6	4	7	3	20	69	11	—	—	80	42	7	2	—	51
1950	10	11	—	—	—	11	16	18	33	11	78	7	6	—	—	13	7	6	1	—	14
1950	11	16	1	1	1	19	30	33	35	27	125	19	7	2	1	29	15	—	—	1	16
1950	12	23	2	—	4	29	25	20	25	26	96	22	6	—	—	28	6	3	—	—	9
1950	13	14	—	1	2	17	11	7	7	16	41	52	26	7	—	85	22	12	—	1	35
1951	1	16	—	—	—	16	13	22	11	19	65	53	31	4	3	91	17	5	—	—	22
1951	2	9	1	—	3	13	12	10	11	17	50	57	27	3	2	89	7	2	—	1	10
1951	3	1	—	—	—	1	9	12	5	8	34	63	32	5	4	104	20	8	—	—	28
1951	4	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—
1951	5	1	—	—	1	2	—	3	2	1	6	58	56	5	1	120	37	14	1	—	52
1951	6	—	—	—	—	—	—	2	—	—	2	46	54	5	2	107	32	25	2	1	60
1951	7	1	—	—	—	1	—	—	—	—	—	24	14	1	—	39	32	31	1	1	65
1951	8	1	—	—	—	1	—	—	—	—	—	46	7	—	—	53	69	11	—	—	80
1951	9	5	—	—	1	6	2	—	—	—	2	77	10	1	—	88	81	10	1	—	92
1951	10	2	1	—	—	3	—	—	1	1	2	30	10	1	1	42	39	19	1	—	59
1951	11	61	8	—	1	70	8	16	16	21	61	17	8	1	—	26	39	15	4	—	58
1951	12	21	1	1	1	24	19	15	8	15	57	29	15	2	1	47	36	13	1	—	50
1951	13	5	—	—	—	5	7	8	19	44	78	16	13	1	1	31	20	5	—	—	25
1952	1	2	—	—	—	2	15	24	23	33	95	75	52	14	13	154	28	7	2	—	37
1952	2	—	—	—	—	—	3	4	9	17	33	48	32	12	16	108	31	6	—	2	39
1952	3	—	—	—	—	—	2	4	—	3	9	40	19	5	1	65	48	12	1	—	61
Total		195	14	3	14	226	199	211	213	262	885	1196	517	97	55	1865	883	248	29	7	1167

*T = Total of rabbits in each Group.

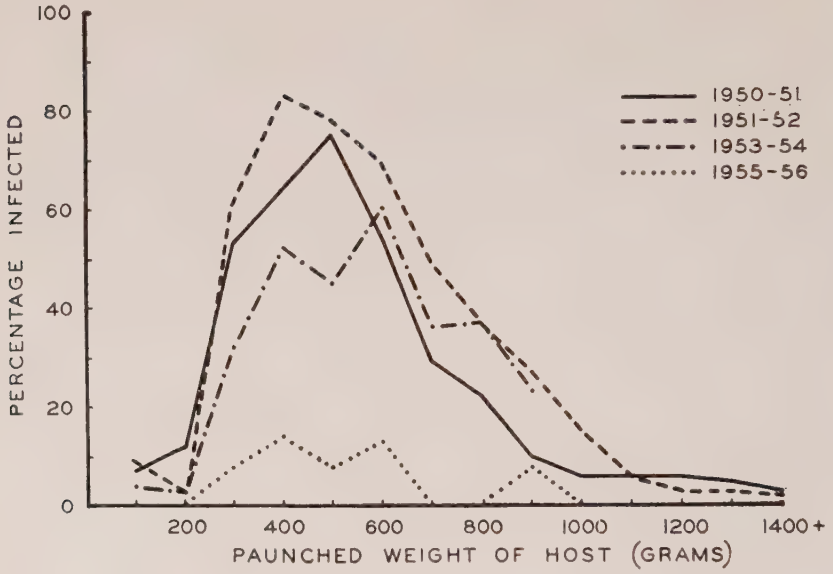

FIG. 9.—Comparing the age-incidence of substantial *E. stiedae* lesions at Gwavas in four different years.

TABLE 6.—Prevalence of Liver Lesions at Gwavas 1953-56.

Year	1953-54					1955-56				
Scale of Infection	0	1	2	3	T*	0	1	2	3	T*
Host weight (g)										
100	23	—	—	1	24	5	—	—	—	5
200	25	4	—	1	30	6	—	—	—	6
300	12	1	2	4	19	12	—	1	—	13
400	6	4	4	7	21	10	2	1	1	14
500	7	4	2	7	20	10	2	1	—	13
600	5	7	8	10	30	11	3	2	—	16
700	11	16	9	6	42	16	3	—	—	19
800	14	10	7	7	38	16	4	—	—	20
900	5	5	2	1	13	18	5	2	—	25
1,000	3	—	1	—	4	26	3	—	—	29
1,100	—	—	—	—	—	34	4	—	—	38
1,200	—	—	—	—	—	33	3	—	—	36
1,300	—	—	—	—	—	16	—	—	—	16
1,400	—	—	—	—	—	2	—	—	—	2
Total rabbits	111	51	35	44	241	215	29	7	1	252

*T = Total of rabbits in each Group.

namely, 1950-51, 1951-52, 1953-54, and 1955-56. Data for the first two years are based on large numbers of rabbits representative of all age classes and all seasons of the year (Tables 3 and 5), but in the two later years examinations were mainly confined to young rabbits (Table 6) collected during the summer months. In 1953-54, samples were collected in October, November, December, and January, while in 1955-56 two samples were obtained in December and February.

Fig. 9 shows that the infection rate of *E. stiedae* varies from year to year, although the differences are of no significance in full-grown rabbits nor in very young ones. The rate of infection with substantial lesions in rabbits of 300g. to 800g increased from 49% in 1950-51 to 60% in 1951-52, and then declined to 43% in 1953-54 and 6% in 1955-56; these differences are significant ($P < 0{\cdot}01$ in each instance). A further sample of rabbits collected in February 1957, contained only 13 animals of 300g to 800g, but as none of these had substantial infections of *E. stiedae* and as there was only one such infection in 12 rabbits of 900g to 1,000g, the infection rate was probably again low in 1956-57. Finally, no lesions at all were found in 16 young rabbits (300g to 800g) collected at Gwavas in November 1957. The general collecting area was the same for all eight breeding seasons (August 1950 to November 1957), and several of the 1950-51 collecting stations provided further samples during subsequent years. Minor locality differences are therefore unlikely to exert any important bias in the pooled data for each year, and are certainly inadequate to explain the very considerable differences between the rates of infection reported above. Possible reasons for these long-term changes in the infection rate of *E. stiedae* will be examined in the discussion.

Fig. 9 is also of interest from the point of view of acquired resistance because there is a suggestion of a relationship between the infection rate in young rabbits (300g to 800g) and the age of peak infection. In 1951-52, the year of highest infection rates, rabbits of 400g were the most heavily infected; whereas, in the previous year (1950-51), with slightly lower infection rates, peak infection was reached in slightly older animals (500g). In 1953-54, infection rates were lower still, and the age of peak infection (600g) was again later although the shape of the age-incidence curve is somewhat irregular owing to the small number of animals examined (Table 6). Finally, in 1955-56, with still fewer young animals and a very low rate of infection, the curve shows no distinct peak at all. These results might be interpreted as indicating that, as the parasite becomes less prevalent, the mean age of initial infection becomes later. However, an alternative explanation is possible. If severe infections cause a substantial drop in the growth rate of the host, then severely infected animals, being light, would be assessed below their true age and there were more such animals in 1951-52 than in later years, thus perhaps depressing the age-weight ratio in 1951-52.

The only other evidence bearing on this problem is provided by samples of rabbits collected at Gwavas in February 1951 (32 rabbits),

and February 1958 (50 rabbits). These animals were all full-grown or nearly full-grown, but had unfused tibiae and were therefore less than 10 months old The infection rate for lesions (all grades) was 31% in 1951 and 6% in 1958 ($P < 0{\cdot}01$), and for oocysts 31% in 1951 and 72% in 1958 ($P < 0{\cdot}01$). It has already been shown that the prevalence of *E. stiedae* was high in young rabbits (300g to 800g) in 1951 but very low in 1955 and subsequent years. The high infection rate with lesions in February 1951 is probably due to the presence of rabbits that had not fully recovered from the severe lesions that developed when the animals were younger. On the other hand, the high infection rate with oocysts and the virtual absence of lesions in the rabbits obtained in 1958 suggests that these animals developed their infections at a later age and that the infections were so mild that few lesions were produced. The age of the rabbits varied from 5 months to about 9 months, but the age-distribution was probably similar in each of the two samples (the mean weight of the rabbits was 1,157g in 1951 and 1193g in 1958). It seems, therefore, that the age of maximum infection with *E. stiedae* is related to the availability of oocysts, but this must be regarded as a tentative conclusion until confirmed by the examination of further material.

(7) *Incidence of Intestinal Species*

THE INFLUENCE OF HOST AGE

Limited data on infection rates for intestinal coccidia are supplied in Tables 7 and 8. The nature of the material examined (preserved rectal faeces) and the limited time available necessitated some grouping of species. Two groups were recognized:

(a) Non-operculate oocysts (mainly *E. perforans* but probably including a few oocysts of *E. exigua*);

(b) Operculate oocysts (including all species except those in (a) above, the most abundant species being *E. piriformis, E. flavescens* and, in young rabbits only, *E. stiedae*).

The first group is referred to below as *E. perforans* (since most of the non-operculate oocysts examined were of that species) and the second group as *Eimeria* spp.

Fig. 10 shows the relationship between host weight (age) and the infection rates (grades 2 + 3) of *E. perforans, Eimeria* spp., and *E. stiedae* in rabbits collected at Gwavas between March 1950 and March 1951. The data were obtained by the examination of rectal faeces for *E. perforans* and *Eimeria* spp., and of bile for *E. stiedae*. The small number of rabbits available in some age groups necessitated the use of 200g weight groups instead of the 100g groups used earlier for *E. stiedae* (Fig. 5). All three curves have a similar shape and reach peak values in the 400g to 599g weight group (rabbits 8 to 10 weeks old), but, with increasing host age, the curve for *E. stiedae* declines more rapidly than that of *E. perforans* and much more rapidly than that of *Eimeria* spp.

TABLE 7.—Infections of Intestinal Coccidia in Relation to Host Weight (Gwavas, 1950-51).

	E. perforans										*Eimeria* spp.									
Sex of Host	Males					Females					Males					Females				
Scale of Infection	0	1	2	3	Total	0	1	2	3	Total	0	1	2	3	Total	0	1	2	3	Total
Host weight (g)																				
< 200	1	1	2	—	4	2	1	—	—	3	—	2	—	2	4	—	1	1	1	3
200 to 399	2	4	13	12	31	2	7	6	8	23	1	4	5	21	31	2	1	5	14	22
400 to 599	—	3	14	12	29	—	6	18	12	36	—	2	4	24	30	1	1	8	21	31
600 to 799	1	9	19	6	35	—	4	19	8	31	1	11	9	11	32	—	3	19	5	27
800 to 999	6	30	22	20	78	5	29	16	10	60	4	26	25	17	72	1	30	20	5	56
1,000 to 1,199	13	95	53	11	172	10	57	34	13	114	7	73	70	18	168	2	53	37	15	107
1,200 to 1,399	11	116	59	11	197	22	71	20	10	123	6	90	80	20	196	1	74	31	13	119
1,400 to 1,599	8	29	6	2	45	8	20	4	5	37	1	29	12	3	45	2	16	16	1	35
1,600 +	1	5	—	—	6	2	3	—	—	5	1	2	3	—	6	—	3	2	—	5
Total rabbits	43	292	188	74	597	51	198	117	66	432	21	239	208	116	584	9	182	139	75	405

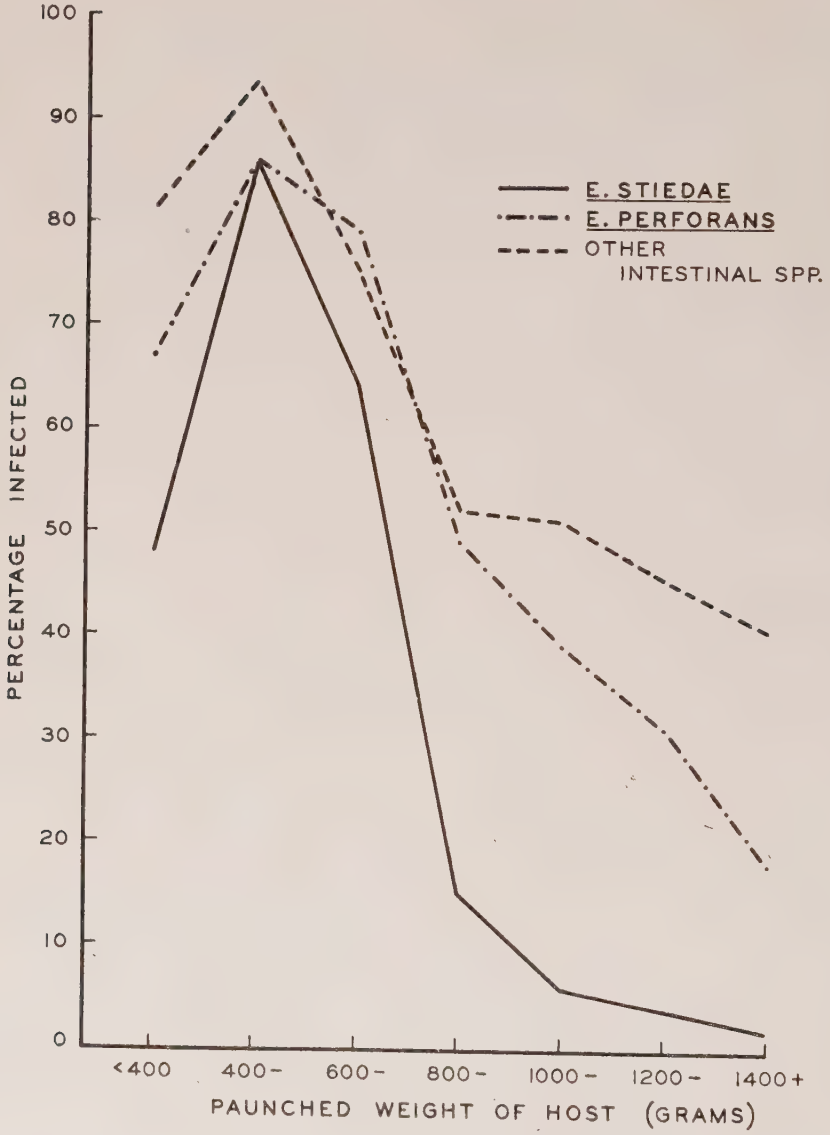

FIG. 10.—Relationship between the infection rate (grades 2+3) of Coccidia (*E. stiedae, E. perforans,* and *Eimeria* spp.) and the weight (age) of the host, Gwavas, 1950-51.

Although the active stages of *E. stiedae* are confined to the liver, the oocysts, like those of the intestinal species, pass to the exterior in the host's faeces. In young rabbits, therefore, the group *Eimeria* spp. is likely to include numerous oocysts of *E. stiedae,* and the presence of

these oocysts may distort the shape of the age-incidence curve for the remaining species in the group. The infection rate (grades 2 + 3) of operculate oocysts in the faeces of 70 young (under 1,000g) rabbits that contained no oocysts of *E. stiedae* in the bile was 60%, and this is not significantly higher than the 49% found in 398 older rabbits negative for *E. stiedae* ($P = 0{\cdot}10$). The proportion of heavy (grade 3) infections of *Eimeria* spp. in these rabbits was, however, much higher in the younger animals than in the older ones (24% and 9% respectively, $P < 0{\cdot}01$). These facts suggest that the high infection rates shown in Fig. 10 for *Eimeria* spp. in young rabbits are partly caused by the inclusion of oocysts of *E. stiedae,* but even so, heavy infections of the remaining species in the group still tend to be more frequent in young rabbits than in old ones.

Further information on the incidence of intestinal coccidia in full-grown rabbits was obtained by examining the faeces of 28 male rabbits collected at Gwavas in February 1958. These animals are included among those listed in Table 2, age being assessed from the condition of the epiphyses of the tibiae and vertebrae. Of 9 rabbits that were less than 10 months old (unfused tibiae), 8 had substantial infections of *E. perforans* and 9 of *Eimeria* spp. The infection rate (grades 2 + 3) in the older animals was only 26% for both *E. perforans* and *Eimeria* spp. and this suggests that the infection rate of intestinal coccidia continues to decline with age even in full-grown rabbits. This suggestion is in agreement with the results of earlier work (Fig. 10) based on samples of more adequate size but depending on weight of host as a criterion of age.

However, although this correlation with host age exists, it is not so well marked as in *E. stiedae* and heavy infections of intestinal coccidia are sometimes found in quite old rabbits. Of 4 rabbits in the above sample that were at least 3 years old (fused vertebral epiphyses), 2 had heavy infections of *E. perforans* while a third had a heavy infection of *Eimeria* spp.; all the oocysts were of normal appearance. Even in 1950-51, when the infection rate (all grades) of intestinal coccidia was nearly 100% in rabbits of 400g to 599g (Table 7), all of 9 rabbits more than 10 months old collected between January and March 1951 were infected with both *E. perforans* and *Eimeria* spp.; 7 of these were grade 2 infections (one of *E. perforans* and 6 of *Eimeria* spp.) and one was a grade 3 infection of *Eimeria* spp. It seems, therefore, that infections with intestinal coccidia tend to persist over very long periods or, alternatively, that the high infection rate in young rabbits fails to give protection from re-infection in later life. Each of these alternatives is in marked contrast to the situation in *E. stiedae* (Section 2).

The Influence of Other Factors

The sex of the host had no effect on the infection rate of either *E. perforans* or *Eimeria* spp., the figures for substantial infections being, for *E. perforans* 44% in male rabbits and 42% in females, and

TABLE 8.—Infections of Intestinal Coccidia in Relation to Period of Collection (Gwavas, 1950-51).

	E. perforans										*Eimeria* spp.									
Weight of Rabbits	200 to 799g					1,000 to 1,399g					200 to 799g					1,000 to 1,399g				
Scale of Infection	0	1	2	3	Total	0	1	2	3	Total	0	1	2	3	Total	0	1	2	3	Total
Collecting Period																				
3	—	3	1	—	4	12	34	—	—	46	—	—	—	—	—	2	25	8	1	36
4	—	—	—	—	—	15	30	5	1	51	—	—	—	—	—	8	28	9	1	46
5	—	—	1	—	1	1	36	25	5	67	—	—	1	—	1	—	20	33	14	67
6	—	—	—	—	—	1	24	25	5	55	—	—	—	—	—	—	18	22	15	55
7	—	1	—	—	1	5	30	18	7	60	—	1	—	—	1	—	33	22	5	60
8	—	1	1	2	4	1	36	12	5	54	—	2	—	2	4	1	27	25	1	54
9	1	1	7	1	10	5	46	14	2	67	—	—	5	5	10	1	34	29	3	67
10	—	4	10	8	22	9	20	4	4	37	3	2	1	10	16	—	26	11	—	37
11	2	2	16	13	33	—	12	5	—	17	1	5	8	19	33	—	13	3	1	17
12	—	10	21	4	35	1	11	5	2	19	—	4	9	20	33	—	9	5	4	18
13	2	7	2	4	15	3	19	8	3	33	—	4	8	3	15	2	22	7	2	33
1	—	1	9	13	23	—	8	7	7	22	1	2	9	11	23	—	10	8	3	21
2	—	2	13	9	24	2	12	21	2	37	—	1	6	17	24	1	13	18	5	37
3	—	1	8	4	13	1	21	17	2	41	—	1	3	9	13	1	12	18	11	42
Total rabbits	5	33	89	58	185	56	339	166	45	606	5	22	50	96	173	16	290	218	66	590

for *Eimeria* spp. 55% in males and 53% in females. These figures take no account of differences in host age, but, from data presented in Table 7, it can be shown that even in restricted age classes the sex of the host has no significant effect on the rate of infection with intestinal coccidia. This is of interest in that it provides additional grounds for discounting the suggestion (Section 3) that *E. stiedae* has a higher incidence in female rabbits than in males.

An example of a locality difference in infection rates with intestinal coccidia was provided by two samples of full-grown rabbits collected in different parts of the Gwavas area in May 1950. The infection rates (grades $2+3$) of *E. perforans* and of *Eimeria* spp. in a sample of 46 rabbits from the higher part of the forestry area were 54% and 74% respectively, while in a sample of 32 rabbits from better pasture at lower altitude, the comparable figures were 25% and 53%. The difference in the infection rates is significant for *E. perforans* ($P = 0{\cdot}02$) but not for *Eimeria* spp. ($P = 0{\cdot}10$). The rabbits from the better quality pasture tended to be heavier than those from the forestry area, but it is uncertain whether this weight difference is due to age, nutrition, or the effects of parasites.

From data presented in Table 8 it can be shown that there were no consistent seasonal differences in the prevalence of intestinal coccidiosis in samples of young (200g to 799g) rabbits collected at Gwavas from September 1950 to March 1951. This finding is in accordance with that already reported for *E. stiedae* in young rabbits (Section 5). Older rabbits (1,000g to 1,399g) are available in adequate numbers throughout the year (Table 8) and show well-marked seasonal differences in the prevalence of both *E. perforans* and *Eimeria* spp. (Fig. 11). The two top broken lines in Fig. 11 show infection rates (grades $2+3$) for *E. perforans* and for *Eimeria* spp. in the faeces, and the bottom line shows the infection rate (grades $2+3$) for *E. stiedae* in the bile of the same rabbits. It is apparent that the infection rates vary according to the season in which the rabbits were collected: all three curves reach high values in the autumn and then fall to low ones during the winter and early spring. Seasonal variations in the mean age of the rabbits in the different samples is indicated by the solid line in Fig. 11; this line, taken from Watson and Tyndale-Biscoe (1953) shows the proportion of rabbits under 10 months old in samples of full-grown rabbits collected at Gwavas between April 1951 and March 1952. In late winter, the samples contain very few rabbits less than 10 months old, and the mean age of the samples therefore tends to be high. From December onwards, increasing numbers of young rabbits, born six months earlier, reach a weight of 1,000g and enter the sample, thus increasing the proportion of animals less than 10 months old and reducing the mean age of the samples. There is thus a well-marked seasonal difference in the mean age of rabbits weighing 1,000g to 1,399g and, as coccidiosis is more frequent in young rabbits than in old ones (Fig. 10), this is sufficient to explain the seasonal differences in the infection rate of coccidia shown in Fig. 11. Clearly, if season of collection has any direct effect on the

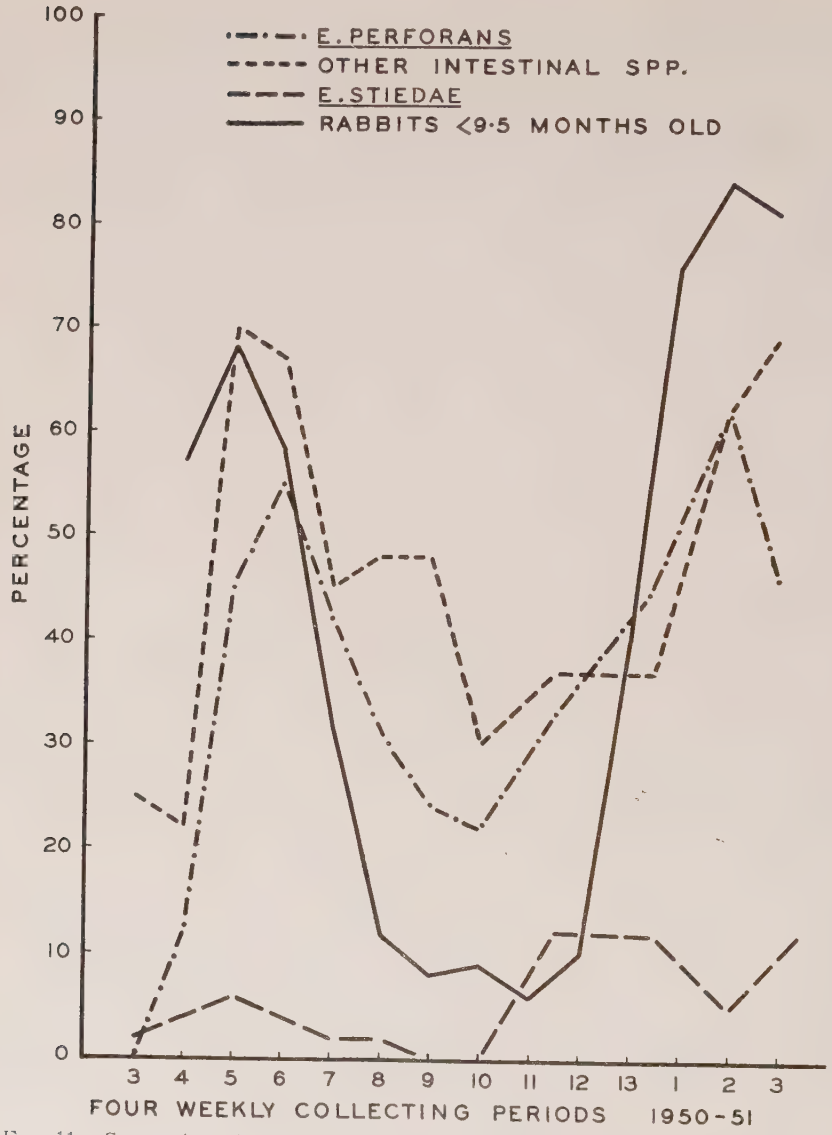

FIG. 11.—Seasonal variations in the infection rate (grades 2+3) of intestinal coccidia and of *E. stiedae* in rabbits of 1,000g to 1,399g, Gwavas 1950-51.

infection rate of the parasite, as distinct from such indirect effects as seasonal changes in host age, then this direct effect must be sought in rabbits of more uniform age.

The number of rabbits examined after March 1951 is inadequate

to reveal long-term changes in the prevalence of intestinal coccidiosis. Only two samples are available, one of 118 rabbits collected in July-August 1956 and the other of 44 rabbits obtained in February 1958; both samples were obtained at Gwavas and consist entirely of full-grown animals. In 1956 the infection rate (grades 2 + 3) was 4% for *E. perforans* and 8% for *Eimeria* spp., the comparable figures for 181 rabbits collected in the same months of 1950 being 32% and 47% respectively. However, the 1958 sample showed relatively high rates of infection (34% for *E. perforans* and 36% for *Eimeria* spp.), although still below those of February 1951 (62% for both *E. perforans* and *Eimeria* spp.). If this latter comparison is confined to rabbits less than 10 months old (35 in 1951 and 21 in 1958), the infection rates (1951 ones in parentheses) are: 48% (63%) for *E. perforans* and 52% (66%) for *Eimeria* spp. It is difficult to interpret the above results because only two samples are available after 1951, and these samples may not have been representative of the district as a whole. However, the infection rates found in 1956 were far below any recorded in 1950-51 (Fig. 11), and it is therefore likely that there was a decline in the prevalence of coccidiosis between 1950 and 1956.

DISCUSSION

Selection of Samples

An important objective of the present work was to measure long-term changes in the prevalence of *E. stiedae,* and this posed the problem of how to distinguish such changes from those due to peculiarities of individual samples. This difficulty was overcome by examining a large number of samples. With the information thus gained, it is now possible to obtain reliable results from fewer and smaller samples of rabbits, providing the animals are selected with regard to uniformity of age and locality of collection.

Rabbits with paunched weights of from 300g to 800g are a convenient age class for use in studying changes in the infection rate of *E. stiedae;* such animals have highest rates of infection, an extreme variation in age of only some 10 weeks, and are available in adequate numbers during most of the breeding season. The group is equally suitable for use in determining rates of infection with intestinal coccidia during the summer months. Rabbits of this age are not available in winter and older animals must then be used. Rabbits with fused tibial epiphyses but unfused vertebral epiphyses are readily available at all times of the year, but may vary in age by some 17 months (R. H. Taylor, pers. comm.). *E. stiedae* is rare in such animals,but the intestinal species, being less affected by variations in host age, still have a fairly high infection rate.

Differences in the infection rate of *E. stiedae,* due to the locality of collection, are usually of small magnitude, and can be overcome by pooling samples obtained from two or more localities. Larger locality differences do sometimes occur, as at Duntroon, but these can be

avoided by confining the collection of material to localities which are similar with regard to moisture conditions, and the density and age-structure of the host population. Infection rates may vary markedly over a period of years, even in a fairly restricted area such as Gwavas, and this means that an infection rate based on a single sample of rabbits in valid only for the time and place at which the sample was collected. Finally, differences in rates of infection are sometimes rather small, though none the less real, and fairly large samples of rabbits are necessary to reveal such differences. Where possible, a sample of at least 50 animals of the required age should be obtained; samples of less than 25 are of little value for demonstrating any but very gross differences in rates of infection.

Causes of Varying Rates of Infection

General Review

The prevalence of coccidiosis is controlled by two main factors: the abundance of the parasite's infective stage (oocysts) and the strength of the host's resistance to infection. The severity of *Eimeria* infection is proportional to the number of oocysts ingested in the initial dose. A relationship of this kind has been reported for *E. stiedae* in domestic rabbits (Becker, 1934, p. 81), for intestinal coccidia of rabbits (Lund, 1949) and for coccidia of other animals, poultry for example (Brackett and Bliznick, 1952). Under field conditions, the size of the initial dose is presumably related to the abundance of oocysts on the pasture, and this value in turn is controlled by the production rate of oocysts (density of infected hosts, period they have been present, and severity of infections) and by the survival rate of the oocysts. The oocysts of most species of *Eimeria* are resistant to the action of many chemical agents and to moderate fluctuations of temperature, although they are susceptible to desiccation (Landers, 1953). Oocysts of ovine coccidia have remained viable up to 10 months in culture (Christensen, 1939), and oocysts of avian coccidia have survived on outdoor plots for 86 weeks (Farr and Wehr, 1949). Oocysts on the ground may be protected from desiccation because high humidities may occur beneath the shelter of grass, even when atmospheric humidity is low (Crofton, 1948).

The resistance of the host to infection may result from past infection with the parasite (acquired resistance) or from other factors such as age or nutrition. Writing of coccidiosis in general, Becker (1934, p. 11) stated that "recent critically conducted experiments have shown almost without exception that susceptible animals may be made to develop a more or less complete immunity to re-infection by the repeated administration of viable sporulated oocysts". The effect of age, as distinct from opportunity to acquire resistance, was investigated by Bachman (1930) using *E. stiedae* in captive rabbits. He was able to produce severe infections in rabbits up to four years old, and concluded that "age of itself does not confer resistance to infection".

Moist conditions have been reported as favouring a high incidence of coccidiosis in hares (Boughton, 1932; Naumov, 1939), but it is not clear whether such conditions affect the ability of the host to resist infection or merely allow a better survival of oocysts. Becker (1934, p. 82), referring to *E. stiedae* in domestic rabbits, stated that infected animals receiving green or succulent feed develop a severe diarrhoea, although this may not occur if dried hay is fed. As another example of the importance of the host's food, Schoop, *et al.* (1954) have shown that vitamin A deficiency can be a predisposing factor in coccidiosis of fowls. Finally, if Chitty's (1955) views on the importance of intraspecific stress as a control agent in vole populations are applicable to rabbits, it could be expected that animals in stressed populations would show less resistance to parasites than those in unstressed populations.

Interpretation of New Zealand Results

Considering again the data collected on *E. stiedae* in rabbits at Gwavas, it seems that at least three different phenomena can be identified, and that no single explanation is adequate for all of them. These are:

(a) In a sample of rabbits collected at a single time and place, the infection rate will be higher in the younger animals than in the older ones.

(b) In samples of rabbits of uniform age, collected in different localities at the same time, the infection rate may be higher in one sample than in the other, as at Duntroon.

(c) In samples of rabbits of uniform age, collected in one general area, the infection rate may vary from one year to another, as at Gwavas.

The first of these situations can be explained on the hypothesis of acquired resistance. This phenomenon is known to occur in rabbits infected with coccidia (Bachman, 1930; Becker, 1934, p. 11), and the infection rate (all grades) of *E. stiedae* in young rabbits at Gwavas in 1950-52 (up to 97%) was certainly great enough to ensure a high level of resistance in the adult population. If the low infection rate of *E. stiedae* in full-grown rabbits is attributed to resistance resulting from the high level of infection in young animals, then perhaps the reverse relationship should also hold, i.e., a low infection rate in young rabbits should lead to a higher rate of infection among full-grown animals if some of these latter escaped infection when they were young. This possibility cannot be tested adequately in the present material because the examination procedure was unsuitable for the detection of mild and transitory infections which might be sufficient to induce resistance. However, there are suggestions that, when infection rates are low, the age of peak infection tends to be late, there is more variation in the age at which rabbits acquire their first infections, and many animals have oocysts without lesions, i.e., light infections (Section 6). While acquired resistance is considered to be the main

factor causing the low infection rate in adult rabbits, it is possible that other factors also operate, and it would be useful to repeat Bachman's (1930) experiments on the effect of age as distinct from opportunity to acquire resistance. It is interesting that the intestinal species of *Eimeria,* unlike *E. stiedae,* continue to show fairly high infection rates even in full-grown rabbits. In this connection, Becker (1934, p. 11) suggested that, for such species, the immunization period is long and that the duration of the immune state is short.

Locality differences in rates of infection, such as those found at Duntroon, are probably due to variations in the availability of oocysts rather than to host resistance. The rabbits examined from the long grass and dry riverbed areas at Duntroon were too young to have already recovered from earlier infections, so acquired resistance is not involved. Variations in resistance due to such factors as crowding or nutrition are likely to be non-specific, yet nematode infestations were heavier in the locality showing a low infection rate for *E. stiedae;* further, the rabbits were all in good condition and had normal deposits of fat. It is therefore improbable that host resistance played any important part in causing the different rates of infection with *E. stiedae.* A greater abundance of oocysts was to be expected on the paddock of grass because conditions there favoured both the production and survival of oocysts. The longer grass would protect the oocysts from desiccation and young rabbits had been present in greater numbers and for a longer period than on the riverbed. However, some of the free living stages of nematodes are also susceptible to desiccation, and the high rates of nematode infestation found in rabbits from the riverbed suggests that humidity remained sufficiently high despite the lack of protecting vegetation. It is probable, therefore, that the age-structure of the host population was the main factor in causing the locality differences in the infection rates of *E. stiedae* at Duntroon. Poor survival of oocysts in low-rainfall districts such as Central Otago (and elsewhere in years of exceptionally low spring rainfall) may cause low infection rates of *E. stiedae,* and material should be collected to investigate this. The present work suggests that, at least in North Otago and in Hawke's Bay, moisture conditions during the winter and early spring are usually adequate to permit the survival of enough oocysts to carry over infection from one breeding season to another. Under such conditions the age-structure of the host population becomes the important factor in determining the level of infection. In *E. stiedae,* which is virtually confined to young rabbits, it is the density of the young animals which is important to the parasite's survival, and the density of the adult rabbit population is of little significance.

The differences from one year to another in rates of infection of *E. stiedae* are probably due to the same cause as the locality differences, i.e., variations in the density and seasonal occurrence of young rabbits. The infection rates (grades $2 + 3$) of *E. stiedae* at Gwavas rose from 1950-51 to 1951-52, and then steadily declined to reach very low levels during 1955-56 (Fig. 9). During much of this period, there was a roughly parallel decline in the density of the rabbit population in this

part of Hawke's Bay (Bull, 1956). Further, the 1951 breeding season was shorter than that of the previous year and fewer young rabbits were born (Watson, 1957). The early termination of the 1951 breeding season caused an increase in the period during which there were few young rabbits to spread infection. This, and the subsequent decline in the density of the rabbit population, including young rabbits, probably caused a reduction in the availability of oocysts of *E. stiedae*. Most of the young rabbits born during the 1952 and later breeding seasons would therefore acquire only small doses of oocysts and thus develop mild infections. This in turn would lead to a reduced production of oocysts and a further decline in the availability of oocysts to later generations of young rabbits. The fact that some of the more recent samples of rabbits, with a very low incidence of coccidiosis, were obtained from restricted areas where rabbits remained quite numerous, does not constitute a serious objection to this hypothesis. The abundance of these rabbits was often due to recent successful breeding, and it might be argued that in such instances the parasite had not had sufficient time to adapt its infection rate to the new level of host density. Similarly, no great importance need be attached to the apparent increase in the infection rate from 1950-51 to 1951-52, when the host population was already declining; the increase was relatively small and the effect of the late termination of the 1950 breeding season (Watson, 1957) might have compensated for the decline in the density of the rabbit population as a whole. It should be remembered, however, that the observed facts could also be explained by a change in the level of host resistance. By analogy with Chitty's (1955) views on the importance of crowding as a cause of population fluctuations in voles, a change in host resistance might be expected to accompany a difference in host density of the magnitude observed at Gwavas. However, in the absence of any evidence to support this view, there can be little value in further speculation along these lines at present—especially as the classical explanation based on host density provides a reasonable explanation for the observed facts.

Effect on the Host

Coccidia as Agents of Mortality

It is known that several species of coccidia can produce fatal infections in rabbits if the oocysts are ingested in large numbers. This has been shown experimentally for *E. stiedae* and *E. perforans* (Bachman, 1930), for *E. magna* (Becker, 1934; p. 87), and for *E. media* (Pellérdy and Babos, 1953). Coccidiosis has sometimes caused considerable losses among hutch-reared rabbits (Chapman, 1929; Becker, 1934, p. 1). Very severe lesions are frequently found in young wild rabbits (Fig. 3 and Stephens, 1952) and occasionally such animals are found dead or nearly dead (Southern, 1940; Bull, 1953). It is clear, therefore, that coccidiosis is sometimes a cause of death in young

rabbits, both in captivity and in the field. The frequency of such deaths and their significance to the population dynamics of wild rabbits can be assessed with much less confidence.

THE EXTENT OF MORTALITY IN WILD RABBITS

Tyndale-Biscoe and Williams (1955) collected data on survival rates of rabbits at Gwavas during the 1951-52 breeding season, and, by comparing their results with those of the present author on the age-incidence of *E. stiedae,* found a significant rise in the survival rate in young rabbits that had just passed the age of heavy *E. stiedae* infection (rabbits 120 days old, 800g in Fig. 5 of the present paper). That there should be a significant rise in the survival rate just when rabbits cease to be infected with severe coccidiosis provides circumstantial evidence that the parasite was at least partly responsible for the higher mortality in younger animals.

The mortality, irrespective of cause, was 30% per 26-day period up to an age of 120 days and 11% thereafter (Tyndale-Biscoe and Williams, 1955). Coccidiosis cannot cause many deaths in rabbits older than 120 days because such animals are rarely infected with *E. stiedae* and have a lower rate of infection with intestinal coccidia than do younger rabbits. There must therefore be other important mortality agents apart from coccidiosis. Assuming that these other agents operate with equal severity on rabbits younger than 120 days, the mortality due to coccidiosis in such animals might be as much as 19% per 26-day period. A lower mortality rate would be expected in places where *E. stiedae* had a lower rate of infection.

If coccidiosis is important as a cause of mortality in wild rabbits, increased survival of young rabbits might be expected during periods when the infection rate of *E. stiedae* was low. In December 1955, February 1956, and February 1957, the infection rate (grades 2 + 3) of *E. stiedae* in rabbits of 300g to 800g was less than 10%, but the proportion of young rabbits in these samples (65% to 81%) was no higher than the 78% to 88% found in samples collected during the corresponding months of 1951-52, when the infection rate of *E. stiedae* was very high (79% to 81%). This fact does not disprove the findings of Tyndale-Biscoe and Williams 1955) because it is likely that increased survival of young rabbits was balanced by a greater loss through emigration. In 1950-52 when rabbits were numerous over the whole district, the loss of young animals from a given locality by emigration was perhaps balanced to some extent by the arrival of young born in surrounding areas. By 1955-57, however, the rabbit population had been reduced to isolated pockets, and any dispersal that occurred was necessarily in one direction only—away from these pockets—there being no adequate breeding populations nearby to provide replacements. Further progress in understanding host-parasite relationships might be expected from simultaneous studies of the reproduction, mortality, and survival of rabbits in two populations having different levels of parasitism.

EPIDEMIOLOGY OF COCCIDIOSIS IN THE RABBIT

From data presented in the preceding sections, it is apparent that *E. stiedae* is well adapted as a density-dependent factor in the natural control of rabbit populations. The parasite is confined to young rabbits and can therefore become abundant only when the host population includes a high proportion of young animals, i.e., during a successful breeding season. Long breeding seasons provide a continuous supply of young rabbits which, if infected, will deposit further oocysts. Later generations of rabbits will therefore probably receive massive doses of oocysts and develop severe coccidiosis. Conversely, a short breeding season will increase the period that oocysts must survive on the ground before encountering the next generation of susceptible hosts. During this period the number of oocysts on the ground will gradually decline through exposure, ingestion by resistant rabbits, or being washed into situations where they are no longer accessible to rabbits. When young rabbits eventually appear they will encounter relatively few oocysts and develop only mild infections, thus providing relatively few oocysts to infect later generations.

In this way *E. stiedae* is likely to compensate for variations in the breeding success of the host, a successful breeding season leading to increased mortality from coccidiosis and a poor breeding season to a reduced mortality. It is likely, however, that there will be some time lag because the parasite will require time to adapt its abundance to a sudden increase in host numbers. If these speculations are correct, and it has been demonstrated at Gwavas that the abundance of *E. stiedae* tends to follow that of the host, then the present work provides justification for one of the assumptions made by Whittle (1955) in formulating his hypothesis concerning the importance of parasites in causing the periodic declines that have occurred in the rabbit population of New Zealand (Wodzicki, 1950, p. 139).

The epidemiology of *E. stiedae* may throw some light on the problem of why rabbit populations on top-dressed pastures sometimes fail to increase as rapidly as do rabbits on poorer pastures, despite the fact that control measures are often less intense on the top-dressed country. This problem was noted by Wodzicki (1950, p. 114), who suggested that possibly top-dressing created conditions that assisted rabbit control. On the other hand, rabbits on good quality pastures seem to have longer breeding seasons and larger litters than do rabbits on poorer pastures. The samples collected at Duntroon provide an example of this (Watson, 1957), and recent observations in the Rotorua-Taupo district also suggest that pasture improvement may lead to greater productivity in the rabbit population. The apparently contradictory observations of Wodzicki (1950) and Watson (1957) can be understood by reference to the epidemiology of *E. stiedae*. The longer breeding season of rabbits on the top-dressed pastures would lead to a high availability of oocysts, heavy infections in young rabbits, and high mortality. It would be interesting to test this hypothesis by

collecting data on reproduction and coccidiosis in rabbits from heavily top-dressed pastures.

The epidemiology of the intestinal species of *Eimeria* is similar to that of *E. stiedae* in that severe infections are more common in young rabbits (8 to 10 weeks old, 400g in Fig. 10) than in old ones. Young rabbits are thus often infected with several species of *Eimeria* simultaneously, and these multiple infections presumably cause greater mortality than if the infections were acquired singly at different periods of the host's life. On the other hand, the frequent occurrence of intestinal coccidia in adult rabbits means that oocysts are produced at all seasons of the year, and not, as in *E. stiedae,* only when there are young animals in the host population. The abundance of intestinal coccidia is therefore likely to be governed by the density of the host population as a whole and not just by the density of the juvenile population as in *E. stiedae.*

Coccidiosis in Relation to Rabbit Control by Man

It is suggested, from a consideration of the data presented in this paper, that in the past coccidiosis has played an important part in controlling the density of rabbit populations in certain areas and, with other factors, in causing periodic variations in density. Indeed, coccidiosis may have been one of the main factors that kept rabbit populations at a low level in certain districts despite the absence of any organized system of control by man. During recent years, however, there has been a great increase in the intensity and efficiency of rabbit control by man in New Zealand, and the role of coccidiosis requires re-examination in the light of this fact.

With a high infection rate of *E. stiedae* at Gwavas in 1951-52, the mortality in young rabbits from coccidiosis was assessed at some 20% per 26-day period, i.e., about half the rabbits born died of coccidiosis before they reached an age of 120 days. Even with this high mortality, there was a fairly dense population at the end of the breeding season and 80% of the animals were young ones (Tyndale-Biscoe and Williams, 1955). The degree of control exerted by natural factors was thus well below standards acceptable to the rabbit control authorities, and poisoning had to be carried out. In this instance, coccidiosis alone was inadequate to control the rabbit population, but the presence of the parasite still provided some economic advantage. If the animals dying of coccidiosis had lived, two poison treatments would have been necessary, or, if only one was used, then the loss in sheep carrying capacity prior to the poisoning would have been very much greater than it was in 1951-52.

It would be useful to confirm some of the suggestions arising from data presented in this paper. For instance, on top-dressed country rabbits are sometimes held at low population levels, and it has been suggested that coccidiosis, together with other natural control factors, may be important in causing this. If this is so, it means that pasture improve-

ment, desirable in itself, has the additional merit of reducing the cost of rabbit control. Intensive control by man will normally reduce rabbit populations to a much lower level than that achieved by natural factors, and, since the latter are usually density-dependent, they are replaced not supplemented by such operations as poisoning. Intensive control by man is, however, expensive and more information on the factors of natural control would indicate priorities for rabbit control. Districts where natural control keeps rabbits at a fairly low level could then be left until such time as extermination is practical, and the available human resources concentrated where they are most required.

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SOME RELATIONS TO BE EXPECTED BETWEEN THE DIRECTIONAL SPECTRA OF SWELL OBSERVED AT DIFFERENT TIMES AND PLACES ON THE OCEAN

By N. F. BARBER, Dominion Physical Laboratory, Department of Scientific and Industrial Research, Lower Hutt

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Summary

The character of waves and swell can be summarized by a directional power spectrum. A simple rule allows the spectrum at any place or time to be deduced in whole or in part from spectra measured at other times and places. The waves around a fixed circular storm are discussed in the light of this rule. The appendix discusses the change in form of a wave-group due to dispersion and diffraction.

INTRODUCTION

It is possible in principle to examine the waves existing in some relatively small area of the ocean and to summarize the measurements in the form of a directional power spectrum. Practical methods of making these measurements are not fully developed as yet but it is clear that such a spectrum might be expressed as a polar plot in the manner of Fig. 1. Any point A in this plot represents a simple regular wave train whose direction of travel, θ and whose wavelength L (or else the wave number k) are the polar co-ordinates of the point. The power of the wave, that is the mean square of the elevation it produces, is recorded by a number attached to the point A. Waves produced by wind do not show any sharply defined wavelength or direction. They may be thought of as the sum of an infinite number of regular trains whose directions and wavelengths differ. Each has a vanishingly small power. These trains would be represented by an infinity of points on the plot of Fig. 1. They cannot all be specified individually, but may be described by a power density, or power per unit area of the plot. Measurements on wind waves or swell would aim to find the power density throughout the plot. The distribution of power among the different types of wave could conveniently be expressed by a system of contours of equal power density as suggested in Fig. 1.

Such an analysis might be made at different times and places on the ocean. The resulting spectra would all be different. Nevertheless, waves convey energy and a wave group which is present in a certain region of the ocean at a certain time, will travel and appear in other regions of the ocean at other times. The purpose of the present note

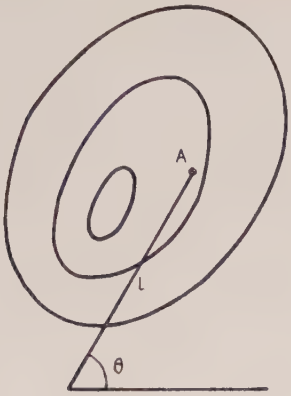

FIG. 1.—A directional power-spectrum.

is to draw attention to the relations which exist between the wave spectra that would be observed at different times and in different regions of the ocean.

The creation of waves by wind is outside the scope of the present paper which applies only to the propagation of waves after they have been formed (swell). Some account might be take nof the attenuation of swell due to energy losses by viscosity or turbulence. At present, however, little is known about such energy losses and in what follows they are ignored. It is also assumed that the progress of each wave train is not affected by the presence of others. This is admissible so long as the resulting slopes of the water surface are not larger than, perhaps, a few degrees.

THE PROGRESS OF A GROUP OF WAVES

Suppose that some large region such as the one shown in Fig. 2 (a) is occupied by a simple regular wave train with crests parallel to A–B. The wave group will progress in the direction normal to A–B with a velocity which is different from that of the wave crests. In the case of waves on water this group velocity, G is half the velocity of the crests and is given by

$$G = gT/4\pi = \sqrt{gL/8\pi}$$

where T is the wave period or L is the wavelength.

It will be assumed that in the course of time the group would move to quite a new position but that there would be no change in the outline of the group or in the height of the waves within it. This is an approximation. Diffraction will cause the group to broaden to some extent, and dispersion will cause it to lengthen. These effects are discussed in the appendix where it is shown that when dealing with large groups of

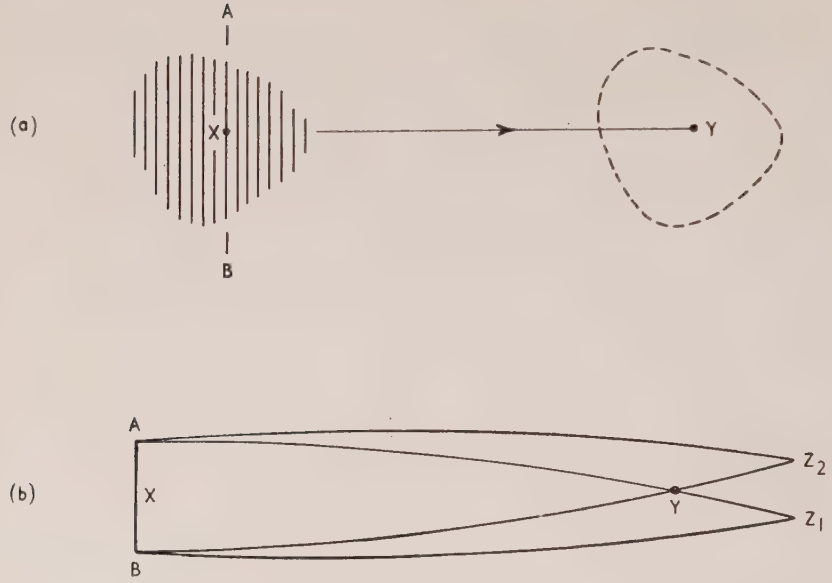

FIG. 2.—The travel of a group of waves. When the curvature of the ocean is considered, waves and wave-groups travel in great circle paths as in (b).

waves such as come from storm areas diffraction and dispersion do not greatly affect the general picture. Consequently, the present discussion is confined to a ray treatment assuming that the waves travel in straight lines or along great circles of the earth's surface normal to the wave fronts, while the wave groups maintain themselves and travel with group velocity.

THE CONNECTION BETWEEN SPECRTA AT DIFFERENT PLACES

Suppose that measurements are being made at a point X when the surrounding sea is disturbed by waves. The waves will not be sufficiently regular to be regarded as a single wave train, but they may be thought of as the sum of very many wave trains. Each wave train may be supposed to extend over the whole disturbed region around X so that each wave train is a large wave-group of the sort that has been discussed.

Consider one of these wave-groups whose orientation and wavelength and consequent velocity are such that having passed X while the measurements were being made, it arrives at a distant point Y in time to be included in wave measurements being made at this new point. We now shall consider what connection may hold between the spectra deduced from the measurements made at X and at Y.

The orientation and velocity necessary to carry the group from X

to Y are not exactly stated. A wave-group has appreciable length and width so that a slightly different orientation and a slightly different velocity would still allow it to appear both at X and at Y. Evidently there will be a whole set of wave groups whose orientations and velocities are in the allowable ranges, and which therefore appear both at X and at Y.

Both measurements will therefore record the same wave-power within this small region of the directional spectrum. In other words, the two spectra will show the same power density in this region.

The conclusion is therefore as follows. If directional wave-spectra are measured at successive times and places along the track of a wave-group, all the spectra will agree in at least one detail. They will show the same power density for a direction and wavelength equal to that of the group.

The same behaviour is shown by swell that propagates over a spherical ocean. Let it be assumed that waves travel on great circle paths. Consider a regular wave train with its crests parallel to the great circle A–B, in Fig. 2b, and travelling to the right. These waves would focus at Z_1 after travelling a distance of 90°. At some intermediate point Y the focussing would have increased the mean square wave height by a factor

$$\sec XY$$

The same is true for waves travelling past X and Y in a slightly different direction and focussing at Z_2. At Y, however, the angle between the directions of travel of these waves is greater than it was at X. In the spherical triangle AYZ_2

$$\frac{\sin AYZ_2}{\sin YAZ_2} = \frac{\sin AZ_2}{\sin YZ_2}$$

The distance AZ_2 is 90° and the angles are small, so the conclusion is that the angle at Y between the wave directions exceeds that at X by the factor

$$\sec XY$$

Because the angles and the wave power change by the same factor, the power density in the directional spectra at X and Y is the same for waves that travel from X to Y in the interval of time between the two measurements.

THEORUM

If wave spectra are measured continually at all points around a closed contour the directional spectrum can be deduced for any point within the contour. This is evident as follows. In the spectrum at a point O

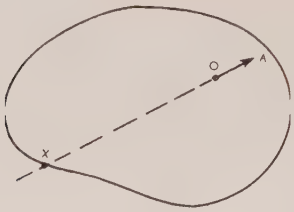

FIG. 3.

in Fig. 3, the power density associated with any wave which travels in the direction OA with a group velocity G is the same as that measured in the spectrum at X at a time earlier by an interval XO/G.

WAVES FROM A LOCALIZED STORM

If the waves from a localized storm are observed continually at all points along some finite line, then the four tangents to the storm boundary, drawn through the ends of the line, enclose a region within which the directional wave spectrum can be inferred.

In Fig. 4, the measurements are supposed to be made continually at all points on the line AB. It can readily be seen that storm waves passing any point in the quadrilateral $PAQB$ must also pass across the line AB and will be observed.

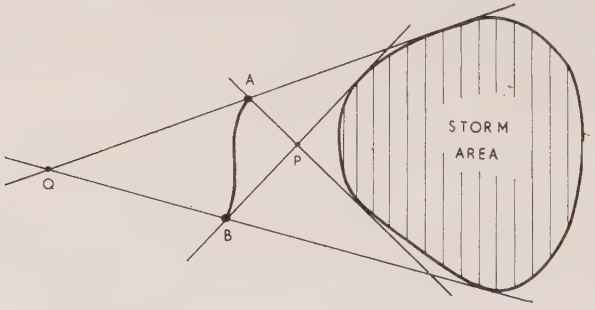

FIG. 4.

On a spherical ocean the four tangents would be great circles. In principle it would be possible for waves to reach Q from the left of the diagram by travelling round the sphere on the "long" path. Even so, they would still be detected and measured as they crossed the line AB at a later stage in their progress. In practice it is not necessary to take account of the "long" path in the travel of swell for all great circle paths on the oceans are interrupted by land masses.

In Fig. 4 the storm is nearer to point P than to point Q, so one may expect to meet higher waves at P .This does not mean that the spectrum

at P will show a greater power density than the spectrum at Q. It means that at P the wave power is incident from a larger arc of directions than it is at Q. This phenomenon is discussed in the next section where the arguments are simplified by supposing that the storm has a circular symmetry.

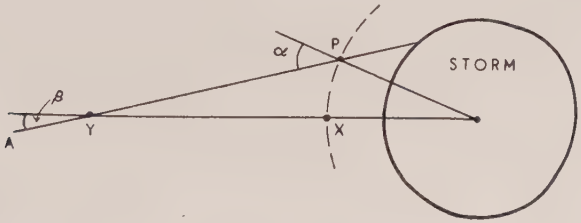

FIG. 5.—A storm with circular symmetry.

A STORM WITH CIRCULAR SYMMETRY

It is the simplest to consider first a storm in which the wind system has a circular symmetry and continues unchanged for a long time. The wave spectra do not then change with time, and at all points which are at the same distance from the storm centre, the spectra are the same providing that the wave directions are measured relative to the line joining the storm centre to the point of measurement.

Consider then the spectra got from measurements at points X and Y in Fig. 5 which are distant x and y from the storm centre. At point Y the waves which travel in a direction YA have passed through some point P which is at the same distance as X from the centre of the storm. In the spectra at Y and at P these waves show the same power density. At point Y they are travelling in the direction β to the radius. At point P they are travelling in a direction α to the radius where

$$\frac{\sin \alpha}{\sin \beta} = \frac{y}{x} \quad \text{(for a "flat" ocean)} \qquad \ldots\ldots\ldots (2)$$

This is true for all possible directions α, and since the spectrum at X is understood to be the same as that at P it follows that if the spectrum is known at a point X at any distance x from the storm centre it can be deduced at any other point Y at a distance y whether y is smaller or greater than x.

The conversion is as follows. Suppose that Fig. 6 (a) represents the spectrum observed at X. Draw a number of radii at convenient angles α_1, α_2 etc. To construct the spectrum at a distance Y calculate the corresponding angles β_1, β_2 etc., for the new spectrum. Then the power densities along the radii at β_1, etc. are the same as in the

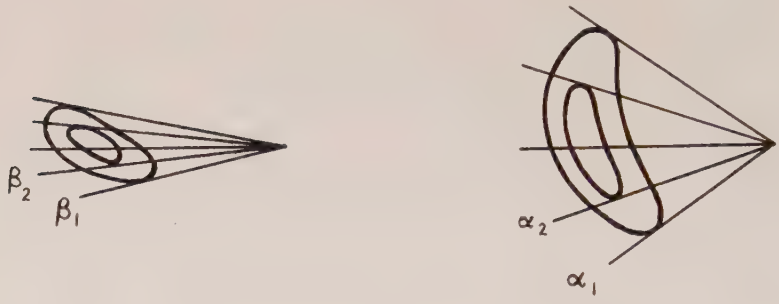

FIG. 6.—The relation between power-spectra measured at Y and X in Fig. 5.

observed spectrum along the radii α_1, etc. The contours of power density observed in the spectrum at X are merely replotted on the new directions to get the new spectrum in Fig. 6 (b).

Although the power densities are the same in the two spectra it is evident that there is less total power in the spectrum at the more distant point because the corresponding angles are smaller in this spectrum.

When the distances are comparable with the earth's radius it is desirable to take account of the earth's curvature by rewriting equation 2 as

$$\frac{\sin \alpha}{\sin \beta} = \frac{\sin y}{\sin x} \qquad \text{..... (3)}$$

As the distance y increase beyond 90° the angles (and consequently the total power in the spectrum) begin to increase. This is the start of antipodal focussing.

ENERGY ATTENUATION

The preceding arguments have assumed that swell does not lose energy by the action of opposing winds or through the "frictional" effect of turbulence in the sea. If, on the other hand, practical measurements show that the power density in the directional spectrum does decrease with increasing distance of travel, this would provide a good measure of the actual dissipation of wave energy.

CONCLUSION

Principles have been indicated on which the directional wave spectra at certain places and times in the ocean might be deduced from spectra measured at other places and times.

A comparison of directional spectra on the path of a group of swell could give a measure of the loss of energy by turbulence or by opposing winds.

APPENDIX

THE CHANGE IN FORM OF A WAVE-GROUP

Consider a wave-group which initially occupies all the quarter lying between the negative axes of x and y. Elsewhere, the water surface is undisturbed. In the quarter occupied by the group, the wave crests are parallel to the y axis and the waves are considered to be advancing in the positive x direction.

The surface elevation in the wave may be written

$$\eta = a \sin kx \qquad \text{..... (4)}$$

and the velocity potential at the surface may be written (Lamb, 1932, Art 229 eq. 11, 12).

$$\phi_0 = g(a/\sigma) \cos kx \qquad \text{..... (5)}$$

These both refer to the initial instant (t zero) and the characters of the wave are, a the amplitude, $2\pi/k$ the wavelength, and $\sigma/2\pi$ the frequency. The wavelength and the frequency are related by the formula

$$\sigma^2 = gk \qquad \text{..... (6)}$$

A velocity potential can be set up by a system of impulsive pressures (Lamb, Art 18), so this wave could be created by applying an impulse of $\rho\phi_0$ per unit area, to a water surface which was originally at rest but had the elevation η. If this action were supposed to take place only in the quarter lying between the negative axes of x and y, then the waves would be created only in this region and would constitute the wave-group.

The subsequent form of the wave-group can be found by adding up the disturbances which spread from eaach infinitesimal region to which the foregoing process has been applied. Thus the fall of a localized elevation whose total volume is unity, produces a circular pattern of spreading waves in which the elevation of the water at a time t and at a distance r from the centre is (Lamb, Art 255 eq. 27).

$$\zeta_1 = \frac{gt^2}{2^{5/2}\pi r^3} \cos gt^2/4r \qquad \ldots\ldots\ldots (7)$$

Alternatively, if a unit total impulse is applied to an elementary area of the surface it gives rise to a circular pattern of spreading waves whose elevation is (Lamb, Art 255, eq. 35)

$$\zeta_2 = -\frac{gt^3}{2^{7/2}\pi\rho r^4} \sin gt^2/4r \qquad \ldots\ldots\ldots (8)$$

These formulae are not exact but they may be used so long as $gt^2 4/r$ is large.

In forming the initial wave-group the volume introduced to an elementary area δA was $\eta\delta A$ and the impulse that was applied was $\rho\phi_0\delta A$. The total elevation which occurs at a point (xy) at a later time t is therefore

$$\eta_1 = \int_{-\infty}^{0}\int_{-\infty}^{0} du\,dv\,(\eta\zeta_1 + \rho\phi_0\zeta_2)$$

$$= a \int_{-\infty}^{0}\int_{-\infty}^{0} du\,dv \frac{gt^2}{\pi r\sqrt{2}} (\sin ku \,.\, \cos gt^2/4r$$

$$- (gt/2r\sigma) \cos ku \,.\, \sin gt^2/4r)$$

$$\ldots\ldots\ldots (9)$$

Here r is the distance from the point (u, v) to the point (x, y).

The group is expected to advance in the positive direction of the x axis with a velocity $\sigma/2k$ so it is convenient at anytime t to refer the position of the point (xy) to a new origin which is displaced form the old one by a distance x_0,

$$x_0 = \sigma t/2k = \tfrac{1}{2}t\sqrt{g/k} = gt/2\sigma \text{ , from (6)} \qquad \ldots\ldots\ldots (10)$$

Write therefore

$$x = x_0 + x_1 \quad y = y_1 \qquad \ldots\ldots\ldots (11)$$

Further, it will appear later that the integral in eq. (9) only grows appreciably from those disturbances which occurred at points (u, v)

displaced from (x, y) by intervals near to (x_0, o). Then, in the integral, it is sufficient to replace r in the coefficients by x_0. With this approximation and with the change of origin noted in eq. (11) and using (10), the elevation at x, y at time t is

$$\eta_1 = \frac{ka}{\pi x_0 \sqrt{2}} \int_{-\infty}^{0} \int_{-\infty}^{0} \sin\,(ku - gt^2/4r)\, du\, dv \qquad \text{..... (12)}$$

It will be noted that

$$r^2 = (x_1 + x_0 - u)^2 + (y_1 - v)^2$$

so the argument in the integral can be written (using eq. 10)

$$ku - gt^2/4r = k(u - x_0^2/r)$$

$$= k\,[x_1 - x_0 - (x_1 - u)^2/x_0 + (y_1 - v)^2/2x_0 - \ldots .]$$

..... (13)

The quantities $(x_1 - u)$ and $(y_1 - v)$ may be treated as the variables and it is proposed to ignore terms of higher order than those shown. The elevation is therefore

$$\eta_1 = \frac{ka}{\pi x_0 \sqrt{2}} \int_{x_1}^{\infty} \int_{y_1}^{\infty} dp\,dq \sin k(x_1 - x_0 - p^2/x_0 + q^2/2x_0)$$

To integrate this expression it is simplest to treat the sine function as the imaginary part of an exponential and to use the nomenclature

$$F(z) \equiv C(z) + i\,S(z) = \int_0^z e^{i(\pi/2)z^2} dz$$

$$F^*(z) \equiv C(z) - i\,S(z) = \int_0^z e - i(\pi/2)z^2 dz$$

This is the Fresnel integral, tabled by Jahnke and Emde (1945). The result is

$$\eta_1 = \text{I.P.of}$$

$$\tfrac{1}{2}\, a e^{ik(x_1 - x_0)} \left[(-\tfrac{1}{2}i)^{\frac{1}{2}} - F^*(x_1\sqrt{2k/\pi x_0}) \right] \left[(\tfrac{1}{2}i)^{\frac{1}{2}} - F(y_1\sqrt{k/\pi x_0}) \right]$$

The wave amplitude is the modulus of this expression and is therefore proportional to the product of the moduli of the two quantities in brackets which depend respectively on x_1 and y_1. The curve of

$$\text{Mod}\ \sqrt{\tfrac{1}{2}} \left((\tfrac{1}{2}i)^{\frac{1}{2}} - F(z) \right) \qquad \text{.....(15)}$$

is shown in Fig. 7. When z is large and positive it tends to zero and when z is large and negative it tends to unity. If the wave-group had advanced by the distance x_0 without any change in form, it would be confined entirely to the quarter between the negative axes of x_1 and y_1. The two factors in x_1 and y_1 show respectively that the group has lengthened somewhat by dispersion and has broadened somewhat by diffraction. At points well inside the group the amplitude has still the value a. Near the nominal boundaries, the x_1 and y_1 axes, the amplitude oscillates somewhat and on the boundaries it falls to $\frac{1}{2}a$. Outside the boundaries the wave amplitude falls gradually away.

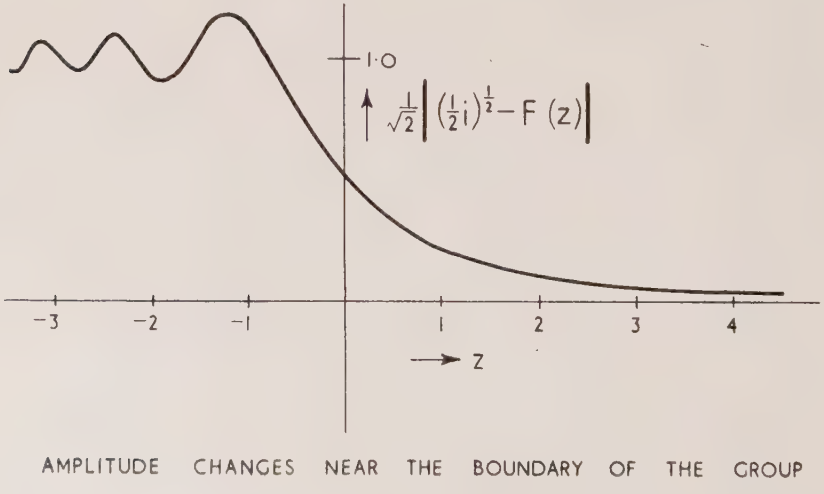

FIG. 7.—Factor of amplitude change near the boundary of a wave-group.

There is now no definite boundary to the wave-group but from Fig. 7 it can be seen that the transition is mainly located in the range of z between ± 2. Thus, the leading edge of this group is blurred by dispersion over a length

$$x_1 = \pm \sqrt{2\pi x_0/k} \qquad \text{..... (16)}$$

and the side of the group is blurred by diffraction over a width:

$$y_1 = \pm \sqrt{4\pi x_0/k} \qquad \text{..... (17)}$$

As regards the form of the waves in the group, it may be noted that at negative values of x_1 and y_1, that is at points within the region nominally occupied by the group, the phase of the factors in brackets show no significant change with position. The phase change with position is almost entirely due to the exponential factor and in consequence the wavelengths inside the group are nearly constant. In front of the group, however, where x_1 is positive the Fresnel factor has a phase which decreases more and more rapidly as x_1 increases. This opposes the normal increase in phase so that the waves grow longer as the distance by which they proceed the group grows greater.

The waves which extend from the side of the group have crests which curve slightly backward. This appears because the Fresnel factor in y_1 has a phase which increases more and more rapidly as y_1 increases beyond zero. As a check on thees results it may be seen that the interval for y_1 in equation (17) is in fact the width of the Fresnel zone within which the path changes by less than a wavelength at a distance x_0.

As a particular example, consider waves of period 10 seconds and wavelength $\frac{1}{12}$ mile which have travelled 1,000 miles. Then the lateral spread is

$$y_1 = \pm \sqrt{4\pi x_0/k} = \pm 13 \text{ miles}$$

This is small compared with the width of a typical storm region in which waves of period 10 seconds could be generated. The forward spreading, x_1, of the wave-group is less by a factor $\sqrt{2}$. Consequently, the spreading of a wave-group as it travels has been ignored in the text. A somewhat different treatment of the problem, by Pierson (1955), leads to similar results.

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INVESTIGATION OF SOME NEW ZEALAND SANDS FOR FOUNDRY MOULDING

By T. E. J. SCAHILL, Dominion Laboratory, Department of Scientific and Industrial Research, Gracefield

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Summary

Physical and chemical properties of a number of natural New Zealand sands have been investigated and compared with American Foundrymen's Society recommended properties, to assess their suitability for foundry moulding purposes.

According to the A.F.S. recommendations, none of the sands investigated could be classified as natural moulding sands. However, by simple conditioning treatments, several of the sands could be conditioned to meet A.F.S. recommendations for specified foundry uses. The majority of New Zealand sands require considerable conditioning to meet foundry requirements.

INTRODUCTION

The majority of foundries in New Zealand use moulding sands from Green Island, Lookout Point, and Parengarenga, and lesser quantities from Mt. Somers and Whitecliffs. The greatest tonnage of castings are made with sands from the Dunedin district. Since this practice involves heavy transport charges, particularly for Wellington and Christchurch foundries, many New Zealand foundrymen are interested in obtaining moulding sand from sources located nearer their works. The present investigation was therefore conducted primarily to assess the suitability of sands from a number of deposits closer to the Wellington and Christchurch foundries.

Data of sand deposits are given in Table 1.

FIELD SAMPLING TECHNIQUES

All bedded deposits were sampled by multiple vertical channelling and channel samples bulked to give approximately one hundredweight of sand. Dune deposits were sampled by removing a 3-inch surface layer over approximately 40 ft × 20 ft area from the leeward side of the dune, and taking the underlying 2 inches of sand to give a sample of about one hundredweight.

This one-hundredweight original sample was later reduced by the alternate shovel method (American Foundrymen's Society, 1952), followed by coning and quartering, to approximately 5 kg.

TEST METHODS

Assessment of the suitability of the sands for foundry moulding purposes was based on the standard A.F.S. procedure, which consists

TABLE 1.

Deposit	Sheet locality Grid reference*	Access	Description of deposit			Dimensions of face sampled (ft)	Samples	Remarks
			Type†	Outcrop	Dip			
Whitecliffs (1)	S74 (Springfield) 354681	Road, 2 miles from Whitecliffs railway station	Bedded, 15 ft coarse sand 10 ft fine sand 15 ft coarse sand 15 ft fine sand	In pit, overlain by 8 ft greywacke gravel	S–E 30°	10 × 30	Taken from top 10 ft of fine sand	Used in foundries as moulding sand
Whitecliffs (2)	S74 (Springfield) 354681	" "	" "	" "	S–E 30°	15 × 20	Taken from bottom 15 ft of fine sand	Used in building industry for plastering
Whitecliffs (3)	S74 (Springfield) 354681	" "	" "	" "	S–E 30°	15 × 30	Taken from top 15 ft of coarse sand	Used in foundries as core sand
Mt Somers (1)	S81 (Mt Somers) 818428	Road, 8 m from Mt Somers railway station	Bedded, 150 ft thick, little variation	In pit, overlain by 10 ft coarse gravel overburden	S–E 35°	160×200	Taken from middle of exposed face	Used in glassworks and in foundries
Mt Somers (2)	S81 (Mt Somers) 818428	" "	" "	" "	S–E 35°	160×200	Taken from bottom 10 ft	Used in glassworks and in foundries
Woolshed Creek	S81 (Mt Somers) 828418	Road, 7 m from Mt Somers railway station	Unconsolidated, variable	In pit, overlain by 20 ft coarse gravel overburden	N–W 5°	4 × 20	Taken from lens 6 ft from top	Used in foundries as moulding sand

*Map Reference—New Zealand Mile Series, scale 1 inch to 1 mile.

†Strata thicknesses given in sequence, top to bottom.

TABLE 1.—*Continued.*

Deposit	Sheet locality Grid reference*	Access	Description of deposit			Dimensions of face sampled (ft)	Samples	Remarks
			Type†	Outcrop	Dip			
Ngapara	S127 (Duntroon) 356848	Road, 1½ m from Ngapara railway station	Bedded, little variation	In pit overlain by 3 ft of soil	—	5 × 10	Taken from 5 ft exposure on side of knoll	Small quantity used in foundry
Pleasant Valley	S102 (Geraldine) 729910	Road, 8 m from Orari railway station	Bedded, 6 ft pebbles 9 ft clay 20 ft sand	In pit overlain by 15 ft quartz pebbles and clay	N–W 5°	5 × 15	Taken from top 5 ft of the sand layer	Has been used in foundries
Windsor	S136 (Oamaru) 265875	Along old railway formation 3 m from Windsor railway station	Bedded 60 ft thick. Interbedded layers of pebbles	In railway cutting overlain by 10 ft of loose overburden	W 12°	60 × 40	Taken from lower 20 ft	No knowledge of having been used
Hedgehope	S169 487313	Private road, 1½ miles from Mako railway station	Bedded 5 ft thick, fine sand	Overlain by a coal seam and underlain by 10 ft of clay	—	5 × 20	Taken from 5 ft of fine sand exposed	
Kokonga	S135 (027° 2 miles from Trig K. 2456 ft (Maniototo Survey District)	Road, ½ m N–W Kokonga-railway station	Bedded, 60 ft sandy clay 10 ft buff clay 25 ft fine sand	In strongly undercut bank at N–E bend of river	N–W 30°	25 × 30	Taken from lower 25 ft of fine sand	
Bannockburn (1)	S133 (010°) 5·8 miles from Round Hill 2635 feet (Bannockburn district, Cromwell sub-division)	Road, 4 miles S of Cromwell	Bedded, 15 ft fine sand 30 ft fine sand 15 ft fine sand 10 ft fine sand 6 ft clay 100 ft sand/grit	In pit near abandoned Cairnmuir coal mine	E 65°	15 × 30	Taken from top 15 ft of fine sand	

TABLE 1.—*Continued.*

Deposit	Sheet locality Grid reference*	Access	Description of deposit			Dimensions of face sampled (ft)	Samples	Remarks
			Type†	Outcrop	Dip			
Bannockburn (2)	" "	" "	" "	" "	E 65°	15 × 40	Taken from middle 15 ft of fine sand	
Landslip Hill	S170 018457	Road, 17 miles E of Gore	Wind blown, 6 ft of coarse sand	On summit of Landslip Hill	—	6 × 50	Taken from 6 ft of coarse sand exposed	
Shepherd Creek	S133 (359°) 2 miles from Round Hill 2635 ft (Bannockburn district, Cromwell sub-division)	Road, 8 miles S–W of Cromwell	Bedded, 100 ft clay 15 ft brown clay 30 ft variable sand 5 ft brown sand	In pit overlain by 15 ft of shales and gravel	W10–20°	30 × 20	Taken from 30 ft of variable sand	
Fairfield	S163 070692	Road, 8 miles S–W of Dunedin	Bedded, 10 ft boulders and loess, 10 ft glauconite sand, 2 ft pebbles, 10 ft sand, 40 ft sand and grit	In pit overlain by 10 ft of soil, boulders, and loess	—	10 × 20	Taken from 10 ft layer of sand exposed	Used in the past in foundries
Blands Bluff	S81 (Mt Somers) 821392	Road, 7 m from Cavendish railway station	Bedded, 20 ft thick, fine sand	In pit overlain by 1 ft clay overburden	—	20 × 20	Taken from 20 ft face exposed	

TABLE 1.—*Continued.*

Deposit	Sheet locality Grid reference*	Access	Description of deposit			Dimensions of face sampled (ft)	Samples	Remarks
			Type†	Outcrop	Dip			
Glentui	S67 700940	Road, 8 m from Oxford railway station (1 m up river)	Bedded, 30 ft thick. Fine sand at base, coarse at upper levels	In river bank, overlain by volcanic rock	S–E	15 × 30	Taken from upper levels about 15 ft from base	
Omihi	S68 228161	Road, 3 m from Omihi railway station	Bedded, 40 ft thick, uniform sand	In pit overlain by 2 ft of soil and clay	S 20°	40 × 50	Taken from lower 20 ft	Used in foundries during 1939–45
Otiake	S127 (Duntroon) 131019	Road, 2 m from Kurow branch railway at Strachans	Bedded, 30 ft sand, 20 ft fine sand and silt	In pit. Overburden not exposed in the immediate vicinity of outcrop	N–E 30°	30 × 20	Taken from top 30 ft	
Maungati	S110 528450	Road, 20 miles S–W of Timaru	Bedded, 60 ft limestone, 80 ft brown sand, 10 ft sandstone, 100 ft sand and pebbles, 40 ft clay and sand	In pit overlain by 200 ft of sand, sandstones and limestone	0°	4 × 20	Taken from a 4 ft layer in lower 40 ft of sand and clay	This deposit has not been worked since 1939
Opoutama	N116/117 521390	Road, ¼ m from Opoutama railway station	Dune deposit	In longitudinal dunes covered in places by soil and grass	Not fnd.	—	Taken from exposed dune 200 yards S–E of railway station	

TABLE 1.—*Continued.*

Deposit	Sheet locality Grid reference*	Access	Description of deposit			Dimensions of face sampled (ft)	Samples	Remarks
			Type†	Outcrop	Dip			
Tutira	N115 368782	Road, ¾ m S of Matahoura viaduct and on left of main State highway	Bedded, 60 ft thick. Part beach and part dune sand	In road cutting overlain by decreasing overburden in direction west	Not fnd.	60×100	Taken from lower 15 ft	
Kairakau	N141 305846	Road, 6 m E of Elsthorpe	Bedded, 15 ft thick. Uniform sand	In pit overlain by shallow earthy overburden	Not fnd.	15 × 30	Taken from 15 ft exposed	Used in foundries as moulding sand
Silver Range (1)	N141 242026	Road, 15 m from Havelock North	Bedded, 10 ft thick. Uniform fine sand	In pit overlain by shallow earthy overburden	Not fnd.	10 × 10	Taken from 10 ft exposed	
Silver Range (2)	N141 204885	Road, 1 m N–W of Elsthorpe	Bedded, 6 ft thick. Uniform fine sand	In pit overlain by thin overburden	Not fnd.	6 × 10	Taken from 6 ft exposed	
Waitomo	N82 535880	Road, 8 miles W of Waitomo	Bedded, 10 ft thick. Uniform sand	In road cutting ¾ m W of Marakopa-Waipa watershed	Not fnd.	10 × 15	Taken from 10 ft uniform sand exposed	
Wanganui	—		—		—	—	Obtained from Blake Engineering Co. Ltd., Wanganui	Used for shell moulding

essentially in measuring a number of chemical and physical properties of known significance in the moulding process. This method was chosen for several reasons:

(1) The procedure is reproducible, standardized, and eliminates personal factors in assessment of sand properties.

(2) The A.F.S. procedure is the system most commonly used and best known by New Zealand foundrymen.

(3) Results can be used to assess the suitability of the sand for various types of moulding, and can be applied to the control of desirable properties by additives, screening, etc. This latter is considered particularly important since, in New Zealand, most foundry sands are used green (undried) without any preparation other than sieving, and with little discrimination as to their suitability for particular foundry purposes.

The methods of measuring the properties are described briefly below.

Moisture Content of Samples for Physical Tests

Determined by drying in an air oven for 1 hr at 105° C. Moisture content is of significance in relation to green strength, dry strength, and permeability, and is therefore determined on mulled samples prepared for the strength and permeability tests.

Permeability

This is expressed as the air flow-rate (ml/min) through a 1 cm cube of rammed sand under a differential pressure of 1 g/cm^2. Permeability is essential in the venting of unwanted gases from castings.

Green Compression Strength

This property is expressed as the stress required (p.s.i.) to crush axially a cylinder 2 in diam. by 2 in long of rammed green (moist) sand. It is of significance, since a sand moulding must have sufficient mechanical strength to withstand handling after ramming.

Dry Compression Strength

Similarly, the dry compression strength is expressed as the stress required (p.s.i.) to crush axially a cylinder 2 in diam. × 2 in long rammed from green sand and subsequently dried at 105° C. This property determines the stability of a sand mould when in contact with hot metal.

TABLE 2.—Chemical Analyses (% Composition)

Sample	SiO_2	Al_2O_3	Fe_2O_3	MgO	CaO	Na_2O	K_2O	TiO_2	H_2O+ (Ign)	H_2O- (105°C)
Whitecliffs (1)	88·3	5·26	1·78	0·28	0·15	0·50	1·70	0·23	1·37	0·28
Whitecliffs (2)	92·5	3·43	0·88	0·13	0·15	0·30	1·40	0·12	0·95	0·39
Whitecliffs (3)	94·3	2·46	0·84	0·09	0·10	0·20	1·00	0·07	0·65	0·24
Mt Somers (1)	99·0	0·32	0·07	Nil	0·06	0·10	0·10	0·03	0·13	0·05
Mt Somers (2)	98·9	0·55	0·07	Nil	0·07	0·10	0·10	0·02	0·24	0·05
Woolshed Creek	98·9	0·48	0·07	Nil	0·10	0·15	0·10	0·06	0·27	0·04
Ngapara	84·8	8·09	1·09	0·15	0·15	2·20	0·90	0·38	1·94	0·44
Pleasant Valley	93·9	3·12	0·43	0·06	0·28	0·90	0·55	0·11	0·66	0·14
Windsor	86·0	8·86	0·40	0·15	0·16	0·80	0·70	0·40	2·41	0·39
Hedgehope	84·6	8·18	0·99	0·20	0·53	1·80	1·30	0·84	1·41	0·42
Kokonga	96·7	1·64	0·19	0·03	0·14	0·05	0·15	0·30	0·53	0·19
Bannockburn (1)	82·0	9·08	1·78	0·57	1·03	2·10	1·40	0·31	1·56	0·44
Bannockburn (2)	80·1	10·2	1·45	0·54	0·99	2·30	1·60	0·34	1·80	0·92
Landslip Hill	99·1	0·14	0·08	0·01	0·06	Nil	0·05	0·08	0·28	0·06
Shepherd Creek	94·0	3·53	0·16	0·01	0·09	1·60	0·05	0·05	0·39	0·09
Fairfield	91·4	4·88	0·61	0·06	0·02	0·40	0·50	0·19	1·61	0·21
Blands Bluff	89·0	6·30	0·48	0·13	0·20	0·90	1·10	0·15	1·48	0·43
Glentui	89·4	4·29	1·58	0·18	0·32	1·00	1·80	0·11	0·90	0·62
Omihi	92·3	3·98	0·45	0·06	0·10	0·70	1·60	0·09	0·51	0·23
Otiake	83·2	8·59	1·35	0·35	0·67	1·10	0·90	0·26	2·22	1·57
Maungati	93·4	3·76	0·18	0·07	0·19	1·20	0·20	0·11	0·63	0·15
Opoutama*	65·6	10·2	12·0	3·40	2·77	2·50	1·20	1·81	0·29	0·25
Tutira†	70·1	12·5	4·35	2·13	3·04	2·80	2·00	0·51	1·47	1·20
Kairakau	74·6	12·3	2·88	0·96	1·29	3·10	2·00	0·41	1·69	0·87
Silver Range (1)	76·9	11·1	2·34	0·67	0·67	2·90	2·70	0·36	1·53	1·16
Silver Range (2)	76·0	11·8	2·33	0·75	0·73	2·90	2·60	0·38	1·45	1·18
Waitomo	73·2	13·9	1·42	0·33	0·38	1·00	3·70	0·25	3·57	2·53
Wanganui	81·7	8·99	1·78	0·66	1·10	2·20	1·80	0·25	1·11	0·45

*MnO 0·3% †MnO 0·1%

"A" Sintering Point

This is the temperature required to sinter the grains of a rammed and dried cylinder of sand, at the point of contact with a superposed, electrically-heated platinum ribbon. The sintering temperature must be sufficiently high to prevent fusion of the sand at points of contact with the hot metal.

Fineness Test

In this test, particles smaller than 20 μ diameter are elutriated out of the sand, and the dried residue is subjected to screen sizing analysis. The sand fineness has an important influence on permeability and other properties.

TABLE 3.—Fineness Test (Samples, as received)

Sample	Tyler screen scale sieves (% retained)										
	14	20	28	35	48	65	100	150	200	270	PAN
Whitecliffs (1)	1·9	1·0	1·2	2·2	3·3	3·5	33·9	37·7	9·7	4·2	1·4
Whitecliffs (2)	1·2	1·2	2·1	5·9	6·9	26·5	41·6	8·3	2·9	1·6	1·7
Whitecliffs (3)	1·9	1·1	1·2	5·2	19·6	33·3	28·1	5·7	1·8	1·3	0·9
Mt Somers (1)	0·4	0·2	0·2	2·6	21·2	30·2	22·5	8·7	4·8	2·9	4·9
Mt Somers (2)	0·6	0·4	1·2	6·3	20·9	31·9	19·2	8·1	4·6	3·1	3·1
Woolshed Creek	0·8	1·0	3·7	15·6	42·1	25·4	6·8	2·4	1·0	0·7	0·4
Ngapara	2·2	0·8	0·9	1·7	2·8	3·4	27·1	39·7	13·2	4·0	3·1
Pleasant Valley	0·2	0·5	1·6	10·9	45·6	31·8	5·3	0·7	0·2	0·1	0·1
Windsor	3·6	2·2	3·0	4·9	5·5	6·0	15·9	34·5	15·6	4·0	3·8
Hedgehope	1·1	1·2	1·3	2·0	3·2	4·9	19·7	40·9	15·7	5·2	4·3
Kokonga	1·7	0·8	0·5	0·5	1·2	8·0	19·4	19·8	13·3	9·4	25·0
Bannockburn (1)	0·3	0·3	0·6	1·7	5·9	31·8	31·8	13·2	5·3	2·4	5·8
Bannockburn (2)	1·4	1·7	2·3	5·4	5·4	17·7	32·0	19·0	8·3	5·7	0·6
Landslip Hill	—	—	0·2	16·2	51·4	23·0	8·3	0·6	—	—	—
Shepherd Creek	0·2	0·2	0·3	0·3	0·3	1·0	12·4	30·0	34·7	11·7	8·6
Fairfield	2·1	2·3	4·0	3·6	3·3	18·4	47·3	12·2	2·4	1·6	1·7
Blands Bluff	4·0	3·5	6·2	11·6	17·6	23·7	20·8	5·6	3·0	2·5	1·0
Glentui	1·7	1·1	1·3	2·6	11·6	36·1	16·3	11·1	6·9	4·6	5·6
Omihi	1·0	0·8	1·6	5·7	14·4	35·4	29·1	7·0	1·8	1·2	1·5
Otiake	7·4	3·9	5·0	5·9	13·6	32·6	17·0	6·0	2·8	2·9	2·9
Maungati	—	—	—	1·6	2·1	2·9	35·7	44·1	8·0	2·4	2·5
Opoutama	—	—	—	0·2	1·8	24·1	48·2	21·7	3·4	0·2	0·2
Tutira	0·3	0·1	0·1	0·2	0·3	0·5	25·7	44·7	18·2	6·5	3·3
Kairakau	1·2	2·3	3·3	4·0	4·3	5·0	28·2	29·0	9·8	5·0	7·4
Silver Range (1)	2·3	3·4	4·6	4·3	4·7	6·3	19·3	29·0	15·4	5·5	4·7
Silver Range (2)	19·8	6·7	5·1	3·1	3·0	2·6	6·0	17·5	16·9	9·2	9·9
Waitomo	4·3	2·3	2·3	3·3	5·7	25·3	32·3	9·3	5·3	3·5	5·6
Wanganui	0·3	0·2	0·3	0·4	2·5	21·6	56·6	14·9	1·9	0·6	0·4

A.F.S. Clay Substance

"Clay substance" is defined as that portion of foundry sand which, when suspended in water, settles at a rate less than 1 in/min. The clay substance is of primary interest in its relation to the bonding properties of a sand.

Grain Fineness Number

The grain fineness numbers is the "average" grain size of the sand, determined by standardized methods from the screen-sizing analysis.

A.F.S. Grain Shape

Grain shapes of the sand are identified by microscopic examination and classified according to a standard system as angular, sub-angular, rounded, or compounded. Grain shape has significant effects on permeability, bonding strength, and casting surface finish.

TABLE 4.—Fineness Test (Samples Washed).

Sample	Tyler screen scale sieves (% retained)										
	14	20	28	35	48	65	100	150	200	270	PAN
Whitecliffs (1)	0·5	0·4	0·4	0·5	0·9	0·2	36·1	29·4	6·6	3·9	6·0
Whitecliffs (2)	—	—	—	—	0·2	7·8	49·6	16·6	5·5	3·4	5·8
Whitecliffs (3)	—	—	—	1·5	14·0	26·7	35·4	8·2	3·1	1·9	3·0
Mt Somers (1)	0·1	0·1	0·1	1·8	17·5	30·5	23·0	9·5	4·7	3·0	6·1
Mt Somers (2)	0·1	0·3	1·0	5·8	20·3	29·8	19·1	8·3	4·4	2·9	4·7
Woolshed Creek	0·4	0·7	2·8	10·7	37·0	31·7	8·4	3·4	1·9	1·0	1·1
Ngapara	—	—	—	—	0·2	0·7	13·5	47·8	19·5	4·6	4·6
Pleasant Valley	0·1	0·1	0·2	2·9	36·8	42·3	9·2	1·9	0·8	0·8	1·2
Windsor	—	—	—	0·1	1·3	3·3	9·2	42·5	21·6	6·1	5·2
Hedgehope	0·1	—	0·1	0·1	0·1	0·2	2·7	41·2	28·4	7·9	9·3
Kokonga	—	—	—	—	0·8	6·2	18·9	19·9	13·4	7·3	28·6
Bannockburn (1)	—	—	—	0·1	2·8	29·4	30·2	12·5	5·7	3·6	5·6
Bannockburn (2)	—	—	—	—	0·3	3·3	23·0	23·6	13·5	7·8	12·5
Landslip Hill	—	—	0·2	7·7	43·2	36·8	9·8	1·3	0·3	0·2	0·1
Shepherd Creek	0·1	—	—	—	0·1	1·0	13·0	33·1	30·3	9·4	8·1
Fairfield	1·0	1·0	2·6	1·6	1·0	10·6	47·1	18·5	3·0	1·3	3·3
Blands Bluff	0·1	—	0·1	1·1	8·2	23·5	23·9	9·8	4·7	3·6	8·0
Glentui	0·1	0·1	0·3	1·0	5·6	31·6	17·4	12·0	8·6	5·9	10·2
Omihi	0·2	0·5	1·6	3·9	14·2	28·7	33·6	8·9	1·6	0·8	2·4
Otiake	0·3	0·1	0·2	0·4	7·8	32·3	19·7	7·3	3·3	2·6	6·3
Maungati	—	—	—	—	0·1	0·4	32·1	47·6	8·9	2·7	2·7
Opoutama	—	—	0·1	0·2	1·9	17·9	52·3	23·3	3·3	0·2	0·2
Tutira	0·2	0·1	0·1	0·1	0·1	0·3	20·7	46·7	20·5	6·4	3·5
Kairakau	0·1	0·1	0·3	0·5	1·0	1·9	23·3	33·1	10·7	4·8	7·7
Silver Range (1)	—	0·1	0·2	0·4	1·0	2·4	6·6	28·2	30·2	10·7	12·2
Silver Range (2)	—	—	—	0·1	0·4	1·3	4·5	20·4	28·3	16·1	19·4
Waitomo	2·2	1·0	1·2	1·9	4·3	17·2	39·1	12·9	5·6	3·0	5·4
Wanganui	—	—	0·1	0·2	1·5	16·5	56·2	20·2	2·1	0·7	0·7

Chemical Analysis

Chemical analyses (which are not required in the A.F.S. test procedure) were included to determine the chemical characteristics of the sands. Foundry sands require a high silica content and a low content of alkalis ($Na_2O + K_2O$), since the presence of readily fusible minerals (such as feldspars) lowers the sinter temperature of the sand.

Screen-sizing Analysis

Although not required in the A.F.S. test procedure, screen-sizing analyses were conducted on sands in the unwashed condition. Since New Zealand foundries receive their sand supplies in the natural condition, this analysis gives a useful check on the source and consistency of supplies as received.

TABLE 5.

	Moisture%	Permeability number*	Green comp. strength P.S.I.†	Clay content%	Fineness No. (A.F.S.)	Sinter temperature ° F‡	Dry comp. strength P.S.I.¶	Grain shape (A.F.S.)
Whitecliffs (1)	6·0	3·0	10·7	15·5	106	2730	100	sub-angular
Whitecliffs (2)	5·7	40	6·0	10·1	94	2640	93	sub-angular
Whitecliffs (3)	5·5	81	2·0	5·2	74	2420§	66	sub-angular
Mt Somers (1)	—	—	—	3·0	82	—	—	sub-angular
Mt Somers (2)	—	—	—	3·4	74	—	—	sub-angular
Woolshed Creek	—	—	—	1·8	52	—	—	sub-angular
Ngapara	5·6	2·0	5·4	8·5	119	2420§	28	compounded
Pleasant Valley	—	—	—	3·7	54	—	—	sub-angular
Windsor	5·7	1·0	8·8	10·5	122	2550§	18	compounded
Hedgehope	6·0	1·0	5·2	10·6	141	2330§	66	sub-angular comp.
Kokonga	—	—	—	4·4	164	—	—	angular
Bannockburn (1)	5·7	1·5	8·5	9·6	80	2370§	64	sub-angular
Bannockburn (2)	5·9	0·5	12·8	15·6	135	2420§	88	sub-angular
Landslip Hill	—	—	—	0·8	48	—	—	sub-angular rnded.
Shepherd Creek	—	—	—	3·7	135	—	—	angular
Fairfield	—	—	—	8·7	82	—	—	angular
Blands Bluff	5·7	2·0	10·5	16·1	96	2420§	95	sub-angular
Glentui	—	—	—	5·9	78	—	—	sub-angular
Omihi	—	—	—	2·9	67	—	—	sub-angular
Otiake	5·5	1·0	17·4	19·2	86	2420	143	angular/sub-anglr.
Maungati	5·5	48	1·8	5·0	102	2510§	32	angular
Opoutama	—	—	—	0·4	76	—	—	sub-angular
Tutira	—	—	—	1·3	112	—	—	sub-angular
Kairakau	5·6	1·0	6·7	16·5	118	2370§	56	compounded
Silver Range (1)	5·5	1·8	5·9	8·3	146	2330§	41	compounded
Silver Range (2)	5·5	1·0	8·2	9·8	170	2330§	73	sub-angular comp.
Waitomo	6·0	1·5	6·9	6·9	87	2370	18	sub-angular comp.
Wanganui	—	—	—	1·8	76	—	—	sub-angular

§These samples showed indications of lack of hot strength as shown in Fig. 9.
*Average of 3 determinations. Maximum deviation from average ±5%
†Average of 3 determinations. Maximum deviation from average ±3%
‡Accuracy claimed ±20° F.
¶Average of 3 determinations. Maximum deviation from average ±4%

TESTING SEQUENCE

Samples (2 Kg) were dried in a laboratory oven at 105° C and stored in a desiccator for 24 hr before testing. Each was subjected to screen-sizing analysis, clay determinations, and then to further screen-sizing analysis (in the washed condition).

The remainder of the sample was mulled dry for 2 min and allowed

to stand 2 min for the dust to settle. Distilled water sufficient to give approximately 5·5% moisture was added gradually (in a 30 sec. period) with the muller rotating, and the sample was mulled for a further 3 min. The sand was then placed in screw-top glass jars and allowed to stand for 2 hr.

Further tests on the mulled samples were then carried out in the following order:

(1) Moisture content.
(2) Permeability.
(3) Green compression strength.
(4) Dry compression strength (oven dried).
(5) "A" sinteringtest.

TEST RESULTS

Results of the above tests are summarized in Tables 2 to 5, inclusive. Grain shapes of several of the most promising sands are illustrated in Figs. 1 to 8.

FIG. 1.—Sand from Maungati. (−28 +100 washed fraction)

FIG. 2.—Sand from Whitecliffs (2). (−28 +100 washed fraction)

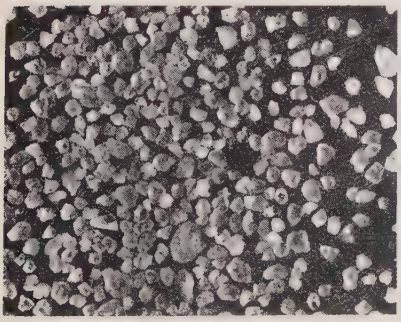

FIG. 3.—Sand from Whitecliffs (3). (−28 +100 washed fraction)

FIG. 4.—Sand from Wanganui. (−28 +100 washed fraction)

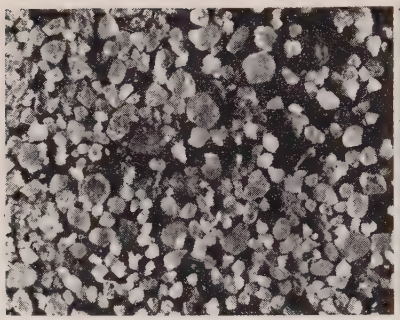

FIG. 5.—Sand from Whitecliffs (1). (−28 +100 washed fraction)

FIG. 6.—Sand from Otiake. (−28 +100 washed fraction)

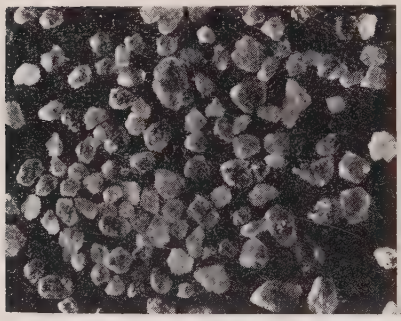

FIG. 7.—Sand from Blands Bluff. (−28 +100 washed fraction)

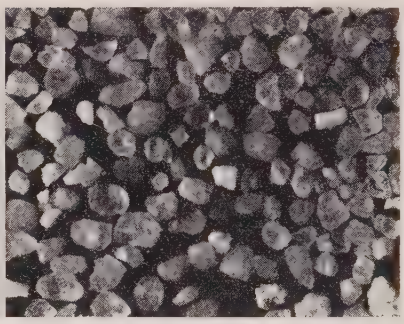

FIG. 8.—Sand from Omihi. (−28 +100 washed fraction)

DISCUSSION

Sand properties recommended by the American Foundrymen's Society (Dietert, 1955; A.F.S., 1944) are given in Table 6 for comparison with the results of the tests on New Zealand sands.

Comparison of the above table with the test results in Table 5 indicated that 11 of the original 28 samples cannot be classed as natural foundry sands owing to unsuitable clay content and fineness number. For this reason, no further tests were conducted on these samples—namely, Mt Somers (1) and (2), Woolshed Creek, Pleasant Valley, Kokonga, Landslip Hill, Shepherd Creek, Omihi, Opoutama, Tutira, and Wanganui. Also, no further tests were conducted on the samples from Fairfield because of the limited quantities of sand available, and from Glentui because of access difficulties, which would make these deposits uneconomical to operate.

TABLE 6.

Castings	Moisture %	Permeability number	Green compress strength (P.S.I.)	Clay substance	Fineness number	Sinter temperature (° F)
Aluminium alloy	6·5–8·5	7–13	6·5–7·5	12–18	225–160	2350
Brass and bronze	6·0–8·0	13–20	7·0–8·0	12–14	150–140	2350
Light grey iron	6·5–8·5	10–15	6·0–7·5	10–12	200–180	2350
Light grey iron (squeeze mlds)	6·0–7·5	18–25	6·0–7·5	12–14	120–87	2400
Medium grey iron (floor)	5·5–7·0	40–60	7·5–8·0	11–14	86–70	2400
Medium grey iron (syn. sand)	4·0–6·0	50–80	7·5–8·5	4–10	75–55	2450
Heavy grey iron (green or dry sand	4·0–6·5	80–120	5·0–7·5	8–13	61–50	2500
Light malleable iron	6·0–8·0	20–30	6·5–7·5	8–13	120–92	2500
Heavy malleable iron	5·5–7·5	40–60	6·5–7·5	8–13	85–70	2500
Light steel (green sand)	2·0–4·0	125–200	6·5–7·5	4–10	56–45	2600
Heavy steel (green sand)	2·0–4·0	130–300	6·5–7·5	4–10	62–38	2700
Steel (dry sand)	4·0–6·0	100–200	6·5–7·5	6–12	60–145	2600

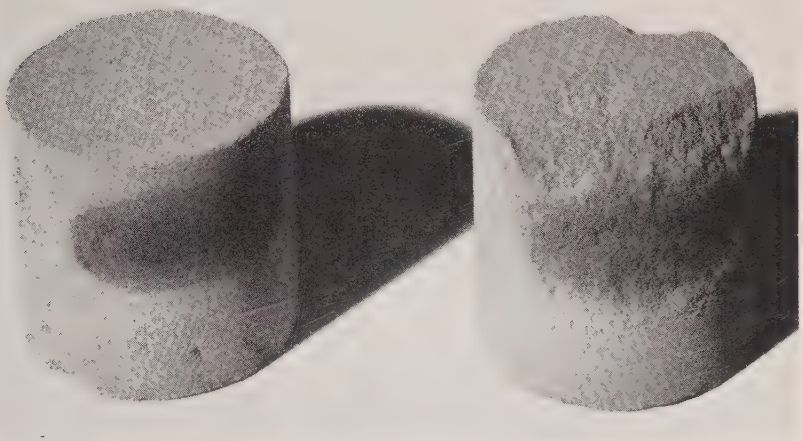

FIG. 9.—Results of "A" sinter test on standard rammed sand sample.

(A) Sufficient hot strength. (B) Lack of hot strength

Although these 13 sands cannot be classed as natural moulding sands, some of their characteristics are prospectively of interest as discussed briefly below.

Mt Somers (1) and (2)

The very low impurity contents of these high-silica sands indicate that they should possess high sinter temperatures and poor bonding properties. Their permeabilities would probably be low owing to the large proportion of pan material as shown in the fineness test results. Hence their use for foundry moulding would require the addition of clay mineral binders after screening for removal of fines.

Woolshed Creek

Similar remarks apply to the send from Woolshed Creek. However, its coarser grain size suggests that, for most foundry moulding purposes, it would require only the addition of bonding clay. Because of its purity and favourable grain size, this sand could be used as an additive for permeability control in other foundry sands.

Pleasant Valley

From the analysis of this sand, a normal, but not high, sinter temperature would be expected. Its coarse grain size suggests possible uses after the addition of bonding clay for heavy grey iron and light steel moulds, and as an additive for permeability control in finer foundry sands.

Kokonga

Owing to its extreme fineness (Table 3), this sand is unlikely to be of practical use as a moulding sand.

Landslip Hill

The purity of this high-silica sand, its coarse grain size and favourable grain shape, indicate that its sinter temperature and permeability should be high. Hence it could be used as a permeability-control additive in finer foundry sands, and, by the addition of suitable bonding material, for steel greensand moulds.

Shepherd Creek

The high proportion of pan material in the fineness test results for this sand indicates a low permeability.

Omihi

In the past, this sand has been used as the basis material for synthetic moulding sands. A reasonably high sinter temperature would be expected from its analysis. The moderate grain fineness number indicates that, after the addition of bonding materials, this sand would be suitable for grey iron moulding.

Wanganui

This sand is used for light grey iron shell moulding. Its chemical analysis indicates a fairly low sinter temperature, which would probably preclude the use of this sand for heavy iron and steel moulds. The sinter temperature and grain fineness number would probably make the sand suitable for medium grey iron moulding after addition of bonding clay.

Opoutama

Because of the very low silica content of this highly impure sand, implying a low sinter temperature, it is not likely to be of practical value for conventional sand moulding.

Tutira

Owing to its low silica content and high content of alkaline oxides, this sand would probably have a low sinter temperature, precluding its use as a basis material for foundry moulding sands.

Fairfield

In the past, this sand was widely used as a natural moulding sand. More recently operation of the Fairfield pit has become difficult and uneconomic, thus eliminating a source of high-purity sand with very favourable moulding properties.

Glentui

As a result of its high silica and low impurity contents, this sand should have a high sinter temperature and, from its screen sizing analysis, a fairly high permeability would be expected if the fines were removed. Unfortunately, in spite of these promising aspects, the Glentui deposit cannot be considered of much practical interest owing to severe access difficulties.

The properties of the remaining fifteen sands—namely, Whitecliffs (1), (2), and (3), Ngapara, Windsor, Hedgehope, Bannockburn (1) and (2), Blands Bluff, Otiake, Maungati, Kairakau, Silver Range (1) and (2) recommended by the A.F.S. for foundry sands, although several of them are being used in New Zealand as natural moulding sands.

However, by relatively simple treatments outlined below, four of these sands could be conditioned to meet A.F.S. requirements:

Whitecliffs (1)

For light grey iron squeeze moulds, this sand shows adequate dry compression strength, slightly high green compression strength, suitable grain fineness number, and adequate sinter temperature. However, its clay substance is slightly high, and its permeability is excessively low. Suitable properties could probably be attained by screening out some of the fines and by adding sand with a larger grain size to obtain the desired clay content, permeability, and green strength.

Whitecliffs (2)

For brass and bronze casting, this sand has adequate green and dry strengths and suitable sinter temperature. The grain fineness number should be increased by the addition of fine sand to control the permeability and to impart to the casting a smooth skin.

Whitecliffs (3)

For medium grey iron floor moulding, the green strength of this sand should be increased to 8 p.s.i. by the addition of a suitable bonding agent, such as bentonite or fullers' earth. Its other physical properties are suitable for this type of moulding.

Maungati

For light malleable iron moulding, this sand would require addition of bonding clay to bring the green strength up to 7 p.s.i. and reduce the permeability, otherwise its physical properties are suitable for this class of moulding.

The remainder of the fifteen sands all developed adequate green and dry strengths, and had sinter temperatures close to those required for a range of moulding purposes. They are, however, unsuitable for moulding in their natural condition, owing to their exceedingly low permeabilities. Screening and additives would be required to develop suitable permeabilities whilst retaining the other properties.

Of the sand deposits tested, those most likely to be of use to Christchurch foundries by virtue of their location and properties are, in order of prospective merit:

Whitecliffs (at present in use)
Maungati (previously used)
Omihi (previously used)
Blands Bluff
Otiake

The only deposit located closely enough to be of interest to Wellington foundries is Silver Range. Sand from this source requires conditioning for general foundry use, to offset its seriously low permeability and low sinter temperature.

CONCLUSIONS

From the foregoing results, it is evident that, according to the A.F.S. specifications, none of the sands tested could be classed as natural moulding sands. However, several of the sands (Whitecliffs (1), (2), and (3), Maungatī) could easily be conditioned for foundry use by small additions of bonding clay, removal of fines, and/or addition of coarser sand.

The sands from Ngapara, Windsor, Hedgehope, Bannockburn, Blands Bluff, Otiake, Kairakau, Silver Range, and Waitomo would require major conditioning treatments (screening and synthetic additions) to develop the permeability values required in foundry sands.

Properties of the sands from Mt Somers, Woolshed Creek, Omihi, Pleasant Valley, Kokonga, Landslip Hill, Shepherd Creek, Opoutama, Tutira, and Wanganui, were not fully assessed, since they all showed very low clay substance. For foundry use, they require additions of bonding clay, and in some cases additional conditioning treatment. Several of these sands (Kokonga, Shepherd Creek, Tutira) have other undesirable properties which are likely to preclude their use in foundry moulding.

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NEW ZEALAND
JOURNAL OF GEOLOGY AND GEOPHYSICS
Volume 1, No. 2, May 1958

CONTENTS

Geophysical Reconnaissance at Kawerau, New Zealand. *F. E. Studt* 219
Pliocene Shell Beds South of the Manukau Harbour. *J. C. Schofield* 247
The Lower Ordovician of Cape Providence: A New Graptolite Zone and a New Species of *Schizograptus*. *S. K. Skwarko* 256
Note on Fault Correlations Across Cook Strait. *G. J. Lensen* 263
Possible Origin of Piercement Structures, Local Unconformities, and Secondary Basins in the Eastern Geosyncline, New Zealand. *J. T. Kingma* 269
The Geology of the Atiamuri Dam Site. *B. N. Thompson* 275
Rationalized Fault Interpretation. *G. J. Lensen* 307
A Borehole Survey of Ilemite-Bearing Beach Sands at Cape Foulwind, Westport. *T. Marshall, R. P. Suggate, and D. S. Nicholson* 318
Petrogenetic Implications of the 1954 Ngauruhoe Lava and its Xenoliths. *A. Steiner* 325
Temperature Distribution about a Cooling Volcanic Intrusion. *W. I. Reilly* 364
Upper Jurassic Fossils and Hydrocarbon Traces from the Cheviot Hills, North Canterbury. *C. A. Fleming* 375
New Zealand Geological Abstracts, 1956. *B. W. Collins* 395

NEW ZEALAND
JOURNAL OF AGRICULTURAL RESEARCH
Vol. 1, No. 3, June, 1958

CONTENTS

Some Effects of MCPB on Establishing Pastures. *D. B. Edmond* 281
Laboratory Methods for Measuring the Toxicity of Pesticides to Honey Bees. *T. Palmer-Jones* 290
The Relationship of *Olpidium brassicae* (Wer.) Dang. to the Big-vein Disease of Lettuce. *P. R. Fry* 301
The Tiller Population of Pastures. *K. J. Mitchell* and *A. C. Glenday* 305
The Influence of Treading on Pasture: A Preliminary Study. *D. B. Edmond* 319
Effects of Flowering on the Root System and Summer Survival of Ryegrass. *Kathleen Soper* 329
Seasonal Growth Relationships in Aberdeen Angus × Jersey Cross-bred Cattle. *M. A. MacDonald* 341
Bloat in Cattle. VIII. Prevention by Pasture Spraying with Anti-foaming Agents. *C. S. W. Reid* 349
The Effect of Thyrozine on Wool Growth and Lamb Production. *I. E. Coop* and *V. R. Clark* 365
Studies in Hogget Rearing. II. The Role of Parasites in Hogget Ill-thrift. *E. A. Clarke* and *Daisy B. Filmer* 382
A Comparison of Phosphatic Fertilizers. *N. A. Cullen* 418

NEW ZEALAND JOURNAL OF SCIENCE

Vol. 1, No. 2, June, 1958

CONTENTS OF THIS ISSUE

Doppler Measurements on Soviet Satellites. *A. H. Allen* and *J. E. Drummond* 143

Sulphur Isotopic Variations in Nature: Part 6—Sulphur Isotopic Measurements on the Discharge from Fumaroles on White Island. *T. A. Rafter, S. H. Wilson,* and *W. B. Shilton* 154

An attempt to Extend the Operating Temperature of Copper Cathode Geiger Tubes. *R. E. Belin* and *A. E. Bainbridge* 172

Coccids Associated with Rata and Kamahi in New Zealand. *J. M. Hoy* 179

The Spectrophotometric Determination of Molybdenum, Tungsten, and Vanadium in Soils and Plants. Part 1. In Soils. *J. H. Watkinson* 201

Podocarpus spicatus Heartwood Extractives. *H. V. Brewerton* 220

Marine Fouling at the Port of Lyttelton. *T. M. Skerman* 224

Immature Stages of *Eriococcus orariensis* Hoy (Homoptera Coccidae). *J. M. Hoy* 258

The Heat Pulse Method for Measuring Rate of Sap Flow in a Plant Stem. *R. L. Closs* 281

Incidence of Coccidia (Sporozoa) in Wild Rabbits *Oryctolagus cuniculus* (L) in Hawke's Bay, New Zealand. *P. C. Bull* 289

Some Relations to be Expected Between the Directional Spectra of Swell Observed at Different Times and Places on the Ocean. *N. F. Barber* 330

An Investigation of Some New Zealand Sands for Foundry Moulding. *T. E. J. Scahill* 342

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